

STUDIES IN LOCOMOTION
AND ANATOMY OF
SCOMBROID FISHES

HARRY L. FIERSTINE

and

VLADIMIR WALTERS

MEMOIRS OF THE
SOUTHERN CALIFORNIA
ACADEMY OF SCIENCES

VOLUME 6

January 18, 1968

STUDIES IN LOCOMOTION
AND ANATOMY OF
SCOMBROID FISHES

STUDIES IN LOCOMOTION AND ANATOMY OF SCOMBROID FISHES

HARRY L. FIERSTINE

*Biological Sciences Department
California State Polytechnic College, San Luis Obispo
and Research Associate in Vertebrate Paleontology,
Los Angeles County Museum of Natural History, Los Angeles*

and

VLADIMIR WALTERS

*Department of Zoology
University of California, Los Angeles*

MEMOIRS OF THE
SOUTHERN CALIFORNIA
ACADEMY OF SCIENCES

VOLUME 6

January 18, 1968

MEMOIRS OF THE SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

The MEMOIRS of the Southern California Academy of Sciences is a series begun in 1938 and published on an irregular basis thereafter. It is intended that each article will continue to be of a monographic nature, and each will constitute a full volume in itself.

Contributions to the MEMOIRS may be in any of the fields of science, by any member of the Academy. Acceptance of papers will be determined by the amount and character of new information and the form in which it is presented. Articles must not duplicate, in any substantial way, material that is published elsewhere. Manuscripts must conform to MEMOIRS style of volume 4 or later, and may be examined for scientific content by members of the Publications Committee other than the Editor or be sent to other competent critics for review.

Because of the irregular nature of the series, authors are urged to contact the Editor before submitting their manuscript.

DONALD J. REISH
Editor

Communications concerning the purchase of the Memoirs should be directed to the Treasurer, in care of the Los Angeles County Museum of Natural History, Exposition Park, Los Angeles, California 90007. Communications concerning manuscripts should be directed to Donald J. Reish, Dept. of Biology, California State College at Long Beach, Long Beach, California. 90804.

Printed by Anderson, Ritchie & Simon, Los Angeles, California

C O N T E N T S

ABSTRACT	1
INTRODUCTION	2
ACKNOWLEDGMENTS	2
MATERIALS AND METHODS	2
RESULTS	9
Acceleration Rates	9
Swimming Analysis	9
Thrust and Caudal Fin Movement	10
Aspect Ratio	11
Osteology	12
Myology	16
DISCUSSION	19
Acceleration Rates	19
Swimming Analysis, Thrust and Caudal Fin Movement	20
Aspect Ratio	23
Osteology	24
Myology	25
Classification	27
SUMMARY AND CONCLUSIONS	28
LITERATURE CITED	30

STUDIES IN LOCOMOTION AND ANATOMY OF SCOMBROID FISHES

HARRY L. FIERSTINE

AND

VLADIMIR WALTERS

ABSTRACT: Acceleration rates, analyses of body movements, and pertinent anatomical features are given for various members of the Scombridae, Istiophoridae, and Xiphiidae and are discussed in light of the modern work on smaller freshwater teleosts and marine cetaceans.

Acceleration values up to 43.1 m/sec^2 are given for *Thunnus albacares* and *Acanthocybium solanderi*. Nearly 100% of the propulsive thrust comes from the caudal fin. There are two main intervertebral joints which are concerned with locomotion, a pre-peduncular and a post-peduncular joint with the body and peduncle held almost stiff, a condition similar to that described for marine cetaceans. The caudal fin achieves its highest transverse speed near or past the axis of progression and the fin's maximum angle of attack occurs before the fin crosses the axis of progression. The caudal fin's angle of attack has an average value of 32.4° as the fin crosses the axis of progression and the average value for all observed fin positions is 29° . Values as high as 100° were attained.

The aspect ratio (span²/surface area) of the caudal fin ranges from 10.26 (*Istiophorus greyi*) to 4.19 (*Xiphias gladius*). The higher values approximate those of efficient, high speed airfoils.

The positions of the joints and the rigidity of the vertebral column are discussed for the Scombridae, Istiophoridae, Xiphiidae, and *Lepidocybium flavo-brunneum*. It is suggested that the retention of autonomous epurals, hypurals, and uroneurals functions to allow camber in the otherwise fused caudal skeleton. The bony peduncular keel is shown to act as a pulley for the great lateral tendons as well as to somewhat stiffen the peduncle and to serve as a support for the fleshy peduncular keels.

Data concerning the shape, length, origin, insertion, and action of the Σ -shaped myomeres are given for the various fishes. Attention is focused on the relative role played by the red and white muscle, the tendons, and the intrinsic caudal musculature in locomotion.

A subordinal classification is presented for the scombroid fishes based upon some of the data presented in this study.

INTRODUCTION

Although certain species of scombroids are the fastest recorded swimming animals (Walters and Fierstine, 1964), little information is available concerning either the anatomical features which pertain to locomotion or the manner in which the body of the swimming scombroid moves. Kishinouye (1923) described the anatomy of the Scombridae but did not relate these features to swimming performance. He did note that tunas and skipjacks swim differently from most other teleosts in that they keep the head and trunk relatively rigid and move the caudal peduncle and caudal fin instead of undulating the entire body.

Nursall (1956, 1958b, 1963a) discussed some of the unique anatomical structures of scombroids and briefly related them to locomotion. He noted that the lateral musculature of scombroids is concentrated in the anterior portion of the trunk and inserts by tendons on the caudal fin so that a large muscular force developed in the trunk is inserted on the small mass of the caudal fin. Furthermore, the shape of the scombroid caudal fin is hydrodynamically efficient for high swimming speeds and since intrinsic musculature is absent from the caudal fin, the shape of the fin cannot be altered.

Kramer (1960) observed that the mackerel (*Scomber scombrus*) swims with pendulum-like movements of the caudal region as do cetaceans, but movement is restricted to the horizontal plane in the fish and to the vertical plane in the mammals. On the basis of experiments with mechanical models, he showed that pendulum movement in the horizontal plane yields the highest swimming velocities when the high aspect ratio fin model is constructed of stiff material and the angle of attack is 20-25°.

In the present study swimming movements of various scombrid fishes have been analyzed and compared with the analyses of swimming offered by Kramer (1960) and by Bainbridge (1963). An anatomical basis is given for these movements and the anatomy is compared with related fishes. In addition, acceleration rates are presented for the wahoo and yellowfin tuna.

ACKNOWLEDGMENTS

Without the cooperation from two different laboratories of the Bureau of Commercial Fisheries, this study would never have been completed. Therefore, we would like to extend particular thanks to Dr. Richard Whitney, his colleagues and assistants from the San Diego Laboratory, for allowing one of us (HLF) to participate in a tuna research cruise during the spring of

1963. Similarly, we wish to thank Dr. John Magnuson, of the Honolulu Biological Laboratory, for making the Kewalo Basin facilities available (to VW) for photographic work.

The services from two local institutions were also invaluable. Mr. John Prescott offered the facilities of the Marineland of the Pacific, Portuguese Bend, California, for photographic work, and Mr. Harold Clemens and his assistants from the California State Fisheries Laboratory, San Pedro, California, helped collect scombrid specimens from the local tuna fleet.

We wish to thank Dr. Boyd Walker and Mr. Wayne Baldwin for allowing us to freely use the fish collection of the University of California, Los Angeles, and Dr. J. R. Macdonald for the use of the skeletal and fossil collections of the Vertebrate Paleontology Department of the Los Angeles County Museum of Natural History, Exposition Park, California. Mr. Aaron Klain, of the Department of Zoology, University of California, Los Angeles, gave advice concerning electronic instrumentation.

Special thanks are due to Mr. Martin Bartlett, of the Woods Hole Oceanographic Institution, for obtaining and sending us two small swordfish. Special thanks are also due Mr. Milton C. Shedd, Mission Bay Research Foundation, who made boat time available to Vladimir Walters.

The bulk of this study was originally submitted by Harry L. Fierstine in partial fulfillment for the Doctor of Philosophy degree at the University of California, Los Angeles. The conversations, advice, and encouragement from fellow graduate students were an unconscious part of the original dissertation, and thus, thanks are due to Drs. Lewis Bishop and Alan Brush, and Messrs. Derek Cleworth, Edmund Hobson, Robert Liu, William Mautner, Howard Reisman and John Wintersteen.

This work was supported by Contract NR 104-669 between the University of California and the Biology Branch of the Office of Naval Research, by National Science Foundation Grant number GB4829, and by U.S. Public Health Service, Zoology Heart Traineeship 5166.

MATERIALS AND METHODS

Nomenclature and General Information on Specimens

Where repeated mention is made to certain fishes, the common name is used instead of the scientific name. Table 1 lists both the common and the scientific names of all species used during the course of our studies.

TABLE 1. Common and Scientific Names

COMMON NAME	SCIENTIFIC NAME	FAMILY
Albacore	<i>Thunnus alalunga</i> (Bonnaterre)	Scombridae
Black skipjack	<i>Euthynnus lineatus</i> Kishinouye	Scombridae
Bluefin tuna	<i>Thunnus thynnus</i> (Linnaeus)	Scombridae
Escolar	<i>Lepidocybium flavo-brunneum</i> (Smith)	Gempylidae
Frigate mackerel	<i>Auxis thazard</i> (Lacepede)	Scombridae
Louvar	<i>Luvarus imperialis</i> Rafinesque	Luvaridae
Pacific bonito	<i>Sarda chiliensis</i> (Cuvier)	Scombridae
Pacific mackerel	<i>Scomber japonicus</i> Houttuyn	Scombridae
Pacific sailfish	<i>Istiophorus greyi</i> Jordan and Everman	Istiophoridae
Sierra	<i>Scomberomorus sierra</i> Jordan and Starks	Scombridae
Skipjack tuna	<i>Katsuwonus pelamis</i> (Linnaeus)	Scombridae
Slender tuna	<i>Allothunnus fallai</i> Serventy	Scombridae
Striped marlin	<i>Tetrapturus audax</i> Phillipi	Istiophoridae
Swordfish	<i>Xiphias gladius</i> Linnaeus	Xiphiidae
Wahoo	<i>Acanthocybium solanderi</i> (Cuvier)	Scombridae
Wavyback skipjack	<i>Euthynnus affinis</i> (Cantor)	Scombridae
White marlin	<i>Tetrapturus albidus</i> Poey	Istiophoridae
Yellowfin tuna	<i>Thunnus albacares</i> (Bonnaterre)	Scombridae

Various works (Amer. Fish. Soc., 1960; Collette and Gibbs, 1962; Fitch and Craig, 1964; La-Monte, 1946; Roedel, 1962, 1963; and Robins and de Sylva, 1960) were consulted for the common and taxonomic names used herein.

Table 2 lists pertinent data concerning the spec-

imens used in the anatomical portion of this study. The identification numbers beginning with the letter S or W refer to either skeletal preparations (S) or specimens preserved in alcohol (W), both which are housed in the fish collection of the University of California, Los Angeles.

TABLE 2. General Specimen Information

NUMBER OF SPECIMENS	LOCALITY AND COLLECTION NUMBER (WHERE APPLICABLE)	TOTAL LENGTH (MM)	STUDY UNDERTAKEN*
<i>Acanthocybium solanderi</i>			
2	Mexico, Tres Marias Ids.	1095-1184	AR, O, M
2	Costa Rica, Cocos I.	1015-1174	AR
2	Mexico, Gulf of California (S329)	?	O
<i>Allothunnus fallai</i>			
1	Calif., Los Angeles Harbor	776	AR, O
<i>Auxis thazard</i>			
6	Fish canneries, San Pedro, Calif.	358-436	AR, O, M
1	Fish canneries, San Pedro, Calif.	440	O
1	Mexico, Punta Angeles	339	AR, O, M
<i>Auxis sp.</i>			
5	Panama (W58-106)	17-110	M
<i>Euthynnus lineatus</i>			
2	Mexico, Punta Santelmo	582-670	AR, M
2	Mexico, Salina Cruz	546-549	AR
2	Costa Rica, Quinones Pt.	435-444	AR
1	9°51.5' N., 85°31.5' W.	315	AR
2	Southern Calif. (S471, S488)	?	O
1	Mexico, Baja California (S83)	?	O
1	Unknown (S93)	?	O
1	Mexico, Tres Marias Ids.	459	M
<i>Katsuwonus pelamis</i>			
11	Fish canneries, San Pedro, Calif.	481-582	AR, M
1	Costa Rica, Puntarenas	679	AR, O, M
1	Costa Rica, Guinos Pt.	647	AR
1	Costa Rica	585	AR, O, M
2	Costa Rica	540-599	AR

NUMBER OF SPECIMENS	LOCALITY AND COLLECTION NUMBER (WHERE APPLICABLE)	TOTAL LENGTH (MM)	STUDY UNDERTAKEN*
<i>Euthynnus affinis</i>			
1	Hawaii, Oahu I. (S84)	?	O
<i>Istiophorus greyi</i>			
1	9°53' N, 85°54' W.	2840	AR
1	Mexico, Gulf of California	?	O
1	Unknown (S549)	?	O
1	Panama (W56-301)	119	M
1	Guatemala (W57-189)	301	M
<i>Lepidocybium flavo-brunneum</i>			
1	Ecuador	940	O, M
<i>Luvarus imperialis</i>			
1	Calif., San Clemente I. (W62-91)	530	AR, O, M
1	Unknown (mounted specimen, Los Angeles County Museum of Natural History)	?	O
<i>Sarda chiliensis</i>			
4	Mexico, Baja California	440-687	AR
1	Mexico, Baja California	?	M
1	Unknown	?	M
2	Southern California	? -411	M
2	California, Santa Monica	430-444	O, M
3	Southern California (S390)	?	O, M
8	Calif., Horseshoe Kelp off San Pedro	440-789	AR
<i>Scomber japonicus</i>			
3	California, Santa Monica	285-310	AR
2	California, Santa Monica	282-313	AR, O, M
25	Unknown (S88)	?	O
1	Southern California	305	O, M
1	Southern California	?	O
2	California, San Clemente I. (S417 S439)	?	O
2	California, Santa Catalina I.	258-375	AR
<i>Scomberomorus sierra</i>			
1	Mexico, Banderas Bay	475	AR, M
2	Costa Rica	597-695	AR, M
2	Costa Rica	581-735	AR
3	Mexico, Baja California, Ballenes Bay (S307)	?	O
1	Mexico, Gulf of California	688	O
<i>Tetrapturus albidus</i>			
1	Rhode Island, Cox's Ledge	2106	AR
<i>Tetrapturus audax</i>			
1	California, San Diego	?	AR, O, M
1	Mexico, Baja California	2348	AR
1	Eastern Pacific Ocean (S281)	?	O
1	Mexico, Gulf of California	2340	O
1	California, San Clemente I.	3245	AR
<i>Thunnus alalunga</i>			
7	Fish canneries, San Pedro, Calif.	659-850	AR
<i>Thunnus albacares</i>			
10	Fish canneries, Sann Pedro, Calif.	541-934	AR
5	Costa Rica, Puntarenas	626-745	AR
1	Costa Rica, Puntarenas	826	AR, O, M
3	Costa Rica, Guinos Pt.	732-982	AR
1	101°44' W., 17°32' N.	724	M
1	California, San Diego	?	O, M
1	Fish canneries, San Pedro, Calif.	?	M
2	Fiji Ids. (S85 S96)	?	O
1	Unknown (S496)	?	O
1	Southern California (S371)	?	O

NUMBER OF SPECIMENS	LOCALITY AND COLLECTION NUMBER (WHERE APPLICABLE)	TOTAL LENGTH (MM)	STUDY UNDERTAKEN*
	<i>Thunnus thynnus</i>		
1	Mexico, Guadalupe I.	1030	AR
	<i>Xiphias gladius</i>		
1	40°52' N., 66°46' W.	3125	AR
1	Azores Ids.	1811	O, M
1	Unknown	?	O
1	California, Santa Cruz I.	2927	AR

*AR = Aspect Ratio; O = Osteology; M = Myology

Two terms used throughout the text are defined as:

Total length: The straight line distance between the anterior-most projection of the snout and the tip of the longest lobe of the caudal fin.

Fork length: The straight line distance between the anterior most tip of the upper jaw (mouth closed) and the tip of the shortest middle caudal fin ray.

Acceleration Rates

Acceleration rates of yellowfin tuna and wahoo were taken from tape recordings of the swimming performance of these fishes. The details concerning the equipment, recording and analytic techniques, and the condition of the fish have already been published (Walters and Fierstine, 1964). The acceleration rates were calculated from the oscillograms with the previously calibrated oscilloscope set at five, two, one, and 0.5 sec/cm sweep rates.

Swimming Analysis

The swimming movements of the wavyback skipjack were recorded on 16 mm ciné film with a Wollensak Fastair camera at 100 frames per sec. The fish were contained in circular pools, 23 feet in diameter and four feet deep, at the Bureau of Commercial Fisheries Honolulu Biological Laboratory, Hawaii. Five dorsal view sequences of one complete tail beat, each taken as the fish swam nearly rectilinear paths, were used in the analysis.

The swimming sequences were projected one frame at a time onto a sheet of paper and the outline of the image of the fish was traced from each frame of the complete tail beat sequence (Fig. 1).

The body outlines for each phase of the tail beat cycle were analysed as follows:

- 1). The fish's axis of progression was established by placing a piece of graph paper under the tip of the caudal fin. For each tracing in a

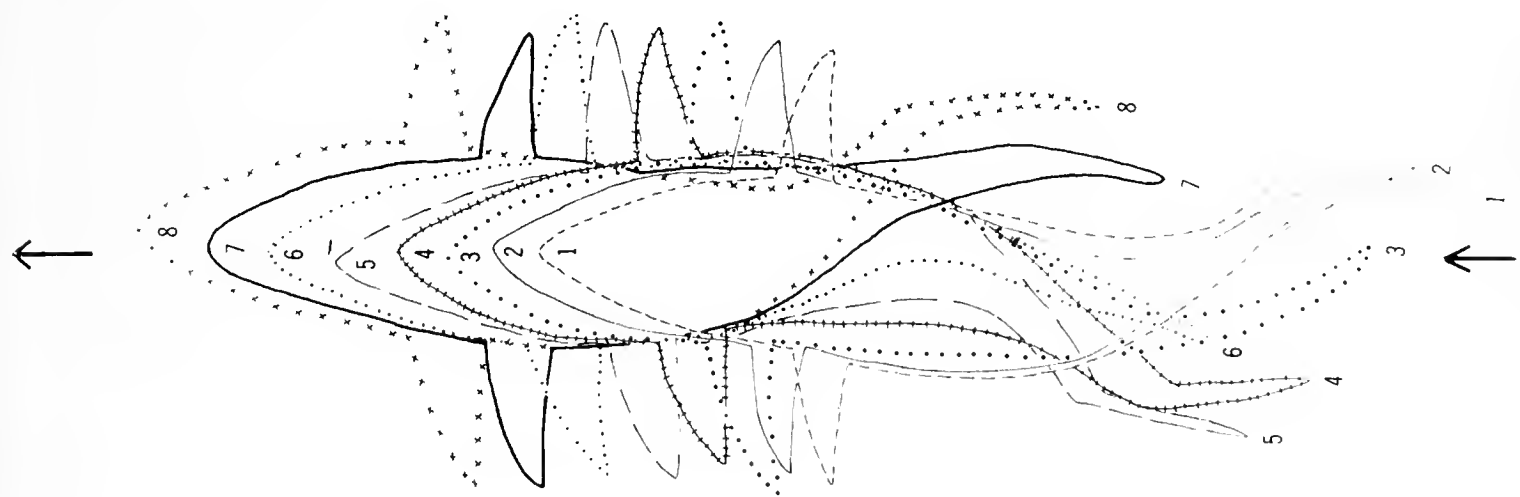


Figure 1. The dorsal outline of wavyback skipjack. Traced from successive ciné frames (camera speed 100 frames per sec) for one complete caudal fin beat cycle. Each outline is rendered separate from the next tracing by a number and a tracing code. Arrows indicate the axis of progression. The swimming speed of this fish is 8.2 body lengths per sec with a tail beat frequency of 14.3 tail beats per sec.

tail beat cycle, a set of coordinates was found for the tip of the tail, and then the average coordinate was calculated. In a similar way, the average coordinate was calculated for the tip of the snout. The straight line distance between the two computed coordinates represented the axis of progression.

2). Although absolute body sizes and swimming speeds of the fish were not measured, swimming speed could be computed in terms of body lengths/sec. Angle of attack and yaw were measured directly.

3). A sheet of graph paper was so oriented on a tracing table beneath the composite body outlines of a swimming sequence, so that the fish's axis of progression was parallel to the ordinate of the graph. The yaw for the different points along the body was read directly from the abscissa and the forward movement was read directly from the ordinate.

The following measurements were made on the swimming sequence tracings:

Body width: The straight line distance between the anterior edges of the bases of the pectoral fins.

Total body length: The length of a line drawn along the midline of the fish from the tip of the snout to the tip of the caudal fin.

Chord length: The straight line distance between the tip of the snout and the tip of the caudal fin.

Angle of attack (Fig. 2): The angle formed between the caudal fin's direction of travel and the fin surface. This value was measured by drawing (by eye) a line tangent to mid-point of the fin's surface, and by drawing another line which connected that point with its position in the next frame. The angle formed by the two lines was measured with a protractor.

Amplitude: The distance between the lateral-most excursion for a given point along the body and the axis of progression (measured perpendicular to the axis of progression) plus the mirror image measurement on the other side of the axis of progression.

The transverse caudal velocity was measured in the following way. The distance (measured perpendicular to the axis of progression) between two successive caudal fin positions was divided by the time taken to travel that distance. This was measured for all fin positions in a tail beat cycle. Since absolute lengths were not known for the ciné films, the measurements were made in arbitrary units.

In addition 16 mm ciné films of swimming

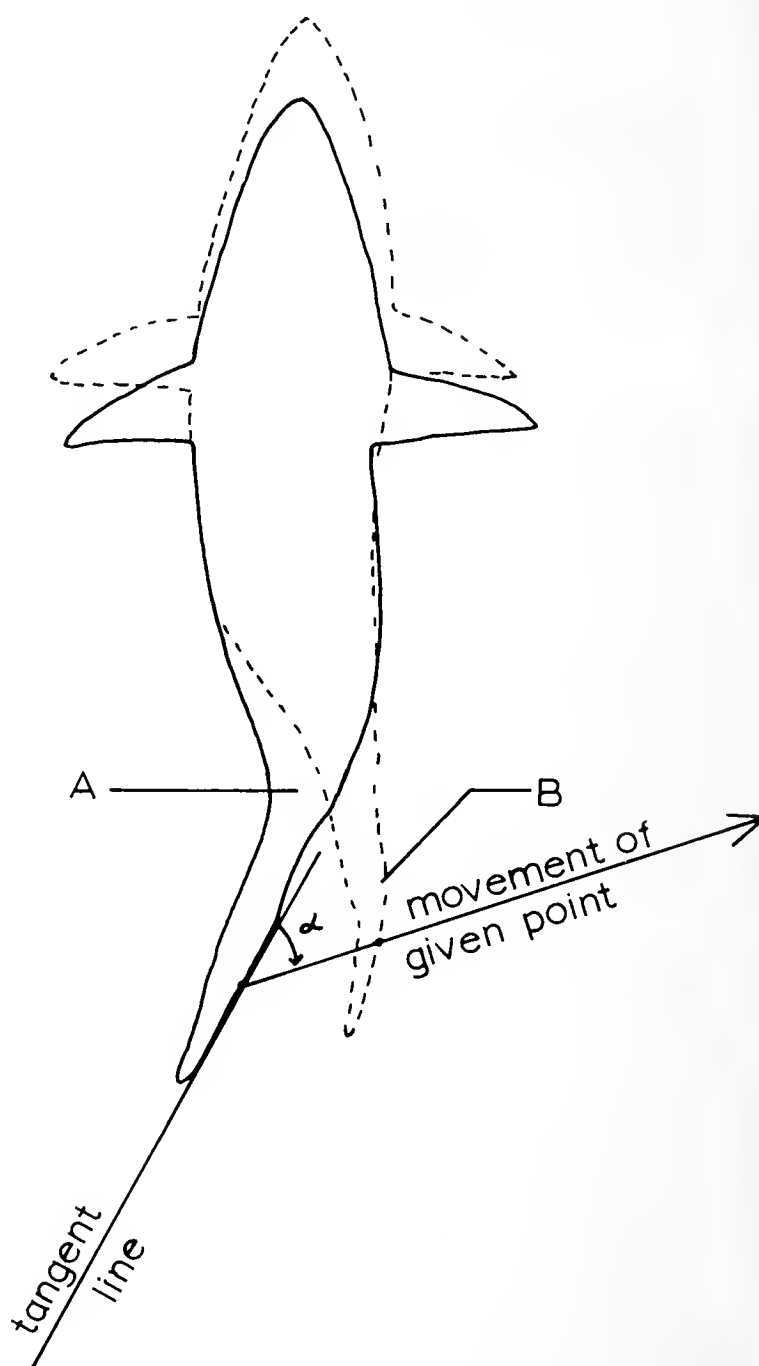


Figure 2. Method of measuring angle of attack (α) and position of pre-peduncular (A) and post-peduncular joints (B). Explanation in text.

Pacific bonito were taken at the Marineland of the Pacific, Portuguese Bend, California. The camera speed was 100 frames/sec.

Consecutive single frame tracings were made of posterior views of the fishes in order to study the dihedral angle of the caudal fin.

Thrust and Caudal Fin Movement

While on a tuna research cruise (sponsored by the Bureau of Commercial Fisheries San Diego Biological Laboratory, San Diego, Calif.), H.L.F. had the opportunity to make observations on living and freshly killed sierra, yellowfin tuna, skipjack tuna, Pacific bonito, black skipjack, frigate mackerel, and wahoo.

Caudal amputations were performed on two yellowfin tuna which were caught on a hand-line

trolled behind a skiff. All handling was done with the fishes' heads submerged in water. The fin-rays were rapidly snipped from the caudal fin with heavy shears and then the hooked fish without caudal rays was returned to the water. The tension on the hand-line was subjectively compared to that developed by similarly handled fish which had intact caudal fins. Two different observers were asked to make subjective evaluations concerning the relative amounts of thrust developed by the amputees and controls.

The caudal fin movement of freshly killed sierra, yellowfin tuna, skipjack tuna, black skipjack, frigate mackerel, and wahoo was studied in the following way. The body of each fish was gripped with one hand and held firmly upright while the thumb and index finger of the other hand gripped the dorsal and ventral surfaces of the caudal peduncle. The peduncle was moved from side to side by hand and associated changes in the attitude of the caudal fin were noted. All movements were performed in air.

Aspect Ratio

The aspect ratio (AR) of the caudal fin is defined as the span²/surface area of one side of the caudal fin (Nursall, 1958b). AR was measured as follows: the caudal fin outline of each fish was traced on a piece of paper with a sharp pencil. The anterior limit of the fin was taken as the line between the leading edges of the anterior-most rays of the dorsal and ventral lobes. An attempt was made to trace the outline of the fin in its expanded condition, which approximated the span in the living state. The span is the straight line distance between the tips of the caudal lobes and was measured to the nearest millimeter. The surface area of the caudal tracing was measured in two ways. It was usually measured with a compensating polar planimeter, but in a few cases the area was determined gravimetrically as follows: the caudal outline was traced onto a good grade of bond paper, and the tracing was then cut out and weighed on an analytical balance (see Ride-wood, 1913 for method). Another piece of the same bond paper of known surface area was also weighed. Thus:

$$\begin{aligned} \frac{\text{weight of paper cutout}}{\text{weight of paper of known area}} \times \text{known area of one side} \\ = \text{surface area of one side of the fin} \end{aligned}$$

The planimetric and gravimetric methods yielded the same surface area values when checked against each other.

The aspect ratio was measured for 93 specimens. Fifty-five of these specimens had been frozen and the caudal outlines were traced after the specimens had thawed. The remaining 38 measurements were made on freshly killed fish.

Myology

All specimens were dissected under a low power microscope or large magnifying lens. The lateral musculature was most easily dissected if the fresh specimen was first wrapped in aluminum foil and boiled in water until all the meat was cooked. Cooking destroys tendons and other collagens and facilitates the dissection of single myomeres. The caudal musculature was best studied when the fish was fresh, without cooking. The large swordfish was steamed in an autoclave.

The relative amount of propulsive musculature was determined by first weighing a freshly killed fish and then weighing the entire lateral musculature (including the skin and tendons) which had been carefully removed with a sharp knife. The weight of the lateral musculature (including the skin weight) was divided by the total body weight and multiplied by 100 in order to determine the percentage of lateral musculature comprising each fish.

The elongation of the myomeres was indirectly determined by counting the number of complete concentric rings in a cross-section of one side of the epaxial musculature. In order to study whether or not the shapes of the myomeres change with growth, young specimens of an unidentified species of *Auxis* were transversely sectioned with a razor blade at the level of the anal opening. The complete concentric rings in the epaxial musculature were counted.

Osteology

Most skeletal material was obtained from the fish collection of the University of California, Los Angeles. Most of this material was originally studied by Godsil and Byers (1944) and Clothier (1950). A large mounted louvar skeleton was studied at the Vertebrate Paleontology Department, Los Angeles County Museum of Natural History, Los Angeles, Calif. Additional skeletal material was prepared by H.L.F. All specimens (except the louvar) are deposited in the fish collection, University of California, Los Angeles.

In order to simplify the vertebral descriptions and to simplify comparisons between species, the vertebral column has been divided into six regions similar to those described by Mago-Leccia (1958).

The six regions cannot be accurately delimited, since the vertebral transformations are gradual. These regions from anterior to posterior are:

1. *Postcranial region* comprises those vertebrae which usually bear stout, compressed, upright neural spines and which lack haemal arches. The first postcranial vertebra articulates with the skull and is often fused to it.

2. *Anterior abdominal region* comprises those vertebrae which bear uncompressed, upright neural spines. Hemapophyses are present, but are not formed into haemal arches.

3. *Posterior abdominal region* comprises those vertebrae which bear uncompressed, upright neural spines. The hemapophyses are formed into haemal arches, but lack haemal spines. Both dorsal and ventral ribs are present.

4. *Anterior caudal region* comprises those vertebrae which bear upright neural spines and the haemal arches bear haemal spines. Dorsal ribs may be present, but the ventral ribs are always absent.

5. *Peduncular region* comprises those vertebrae with depressed neural and haemal arches and spines. In some species, the centra may develop lateral bony keels. Dorsal and ventral ribs are absent. Since the anal finlets are part of the anal fin, the term "peduncular region" is not the same as the "caudal peduncle" as defined by Hubbs and Lagler (1958:25). The scombrid caudal peduncle comprises the posteriormost position of the "peduncular region" plus the vertebral elements making up the "caudal fin complex."

6. *Caudal fin complex* comprises those vertebrae with neural and haemal spines (or their embryological derivatives) which support the caudal fin.

The number of vertebrae comprising each region is subject to some individual variation. Descriptions are based on individuals representative of the species.

For the most part, the nomenclature developed by Gosline (1960, 1961a, 1961b) is used to describe the caudal skeleton. At the suggestion of Elbert H. Ahlstrom (*in litt.*) the last vertebra with its fused hypural elements is identified as the urostyle (= Gosline's terminal centrum).

Two terms concerned with the caudal fin rays are defined as follows (Fig. 14): *Principal caudal fin rays* are those caudal fin rays that attach in any way to the hypural elements of the urostyle. This generally includes 15 branched caudal fin rays plus the one adjacent unbranched caudal fin ray of each lobe for a total of 17 principal cau-

dal fin rays. The *procurrent caudal fin rays* are all those caudal fin rays of each lobe which are anterior to the principal caudal fin rays.

After the muscles had been studied (see above), the remaining flesh was removed with a small brush under running water. Care was taken to keep the skeleton articulated and to keep all the caudal rays attached to the hypural plate. After the specimen had dried, it was ready for study. A few skeletons were prepared by placing them in a dermestid beetle colony, but in general this method of preparation was not too satisfactory.

The "vertebral length gradient" (Ford, 1937) was computed by measuring the anterior-posterior length of each centrum, adding together the values for all vertebrae and dividing the value for each centrum by the total value. This series of calculations gives relative length of each centrum. The relative length of each centrum was then plotted against its numerical position in the vertebral column.

RESULTS

Acceleration Rates

The acceleration measurements for a yellowfin tuna and a wahoo are given in Table 3. The oscillograms from which these values were calculated are given in Figure 3. The vertical distance between two peaks (which represents two different velocities) divided by the horizontal distance between the two peaks (which represents time) equals the acceleration rate.

Swimming Analysis

During steady, rectilinear locomotion all of the wavyback skipjack in the ciné films kept their pectoral and dorsal fins extended. As with most fish, the propulsive movements of wavyback skipjack take the form of a lateral body wave that travels antero-posteriorly. At any given moment only slightly more than one-half of a body wave length or slightly less than a full body wave length, can be seen (Fig. 1) and this body wave has a minimum amplitude near the anterior pectoral base (Fig. 4). The amplitude at the middle of the caudal fin averages 14.3 times greater than the minimum amplitude.

Analysis of the dorsal outline tracings from the ciné films revealed that the body of the wavyback skipjack has two main axial joints concerned with locomotion. One joint is localized at the anterior border of the caudal peduncle (pre-peduncular joint) and the second joint is localized at the anterior border of the caudal fin (post-peduncular

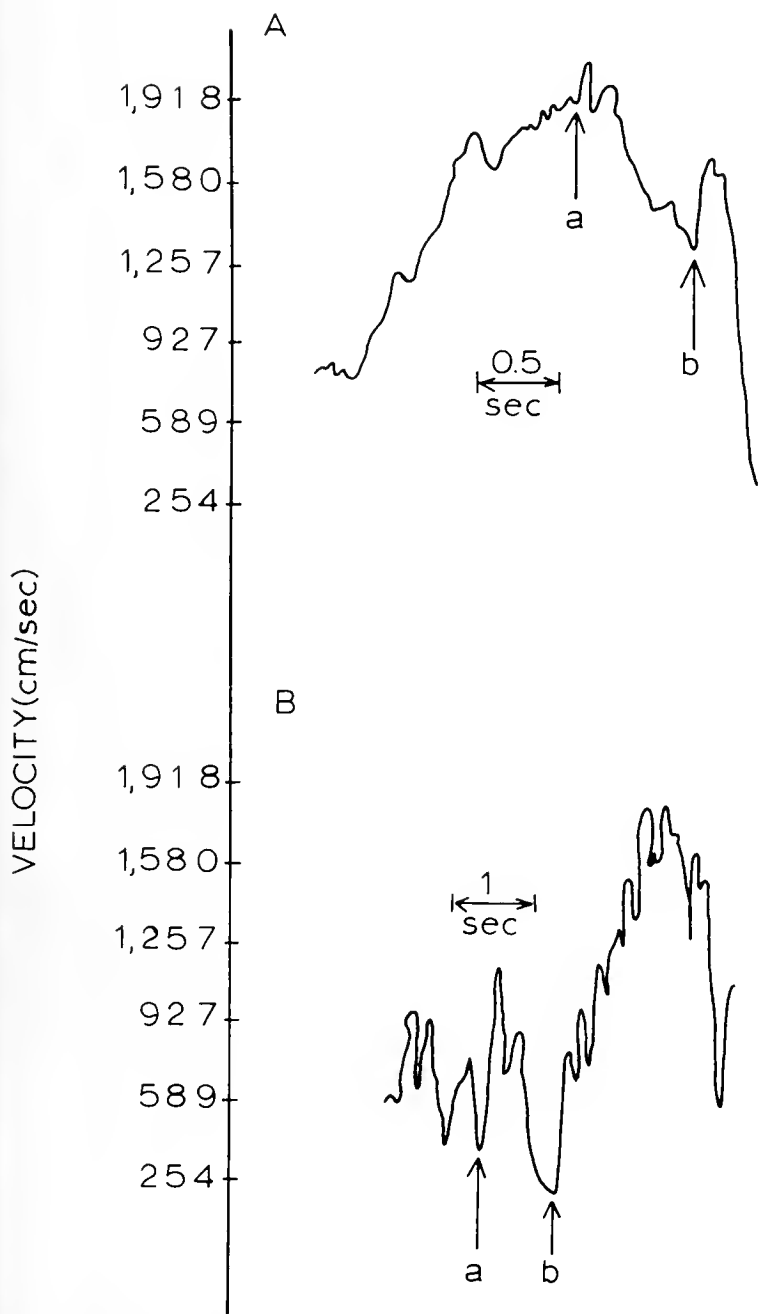


Figure 3. Oscillograms showing acceleration values for a wahoo (A) and a yellowfin tuna (B). Small letters indicate starting velocities for values listed in Table 3.

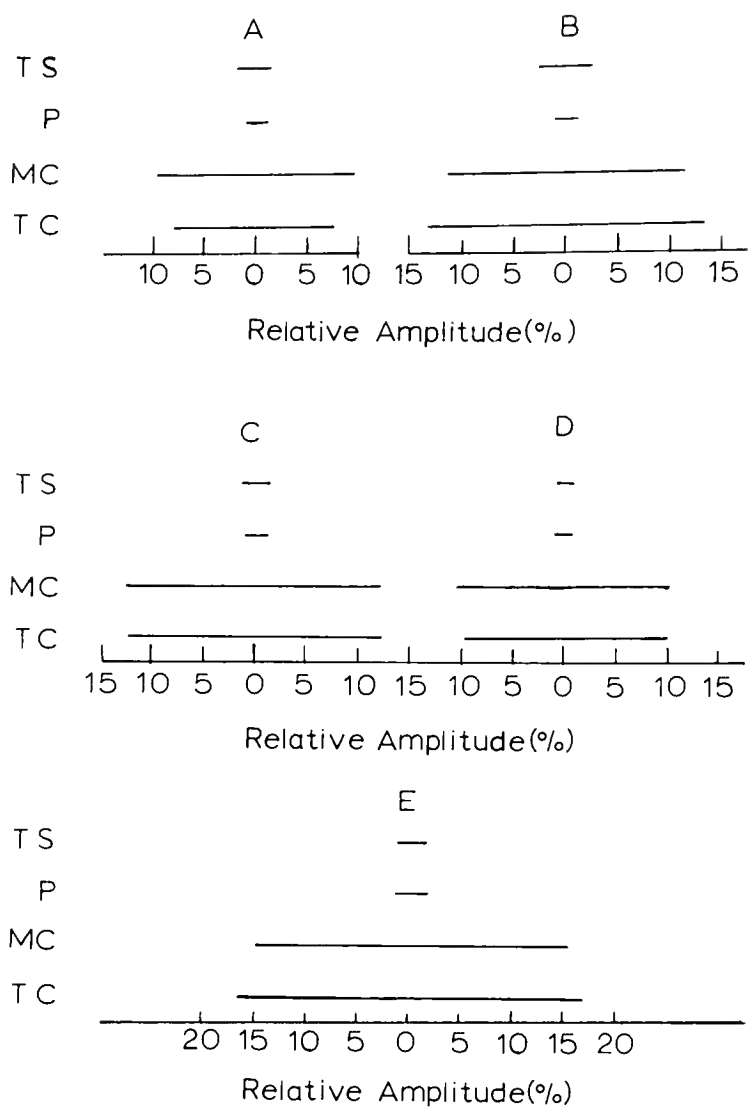


Figure 4. Relative yaw amplitude at various positions along the body in five sequences of wavyback skipjack. All amplitude values are expressed as percentage of total length of the fish. Relative swimming speeds and number of tail beats/sec are: (A) 3.1 body lengths/sec and 7.7 tail beats/sec; (B) 3.8 body lengths/sec and 9.1 tail beats/sec; (C) 4.0 body lengths/sec and 10.0 tail beats/sec; (D) 4.7 body lengths/sec and 12.5 tail beats/sec; (E) 8.2 body lengths/sec and 14.3 tail beats/sec. Abbreviations for the different positions along the body are: TS (tip of snout); P (mid-point between anterior edge of pectoral fins); MC (mid-point of caudal fin); TC (tip of caudal fin).

TABLE 3. Acceleration Values for a Wahoo and a Yellowfin Tuna

FISH	TOTAL LENGTH OF FISH (cm)	DURATION (sec)	START VELOCITY (cm/sec)	END VELOCITY (cm/sec)	ACCELERATION (cm/sec ²)
Yellowfin D	98.0	.19	346.40	1,165.58	4,311.47
Yellowfin D	98.0	.15	204.14	764.45	3,735.40
Wahoo D	113.1	.05	1,902.73	2,082.19	3,589.20
Wahoo D	113.1	.11	1,304.9	1,682.04	3,428.54

joint) (Figs. 1,2). The caudal peduncle was held relatively rigid and the body anterior to the prepeduncular joint developed only a slight curvature.

In general, as the caudal fin oscillates from side

to side, its transverse velocity increases from 0 at the extreme lateral position to a maximal value near or slightly beyond the axis of progression and drops to 0 at the other extreme lateral position (Fig. 5). The angle of attack is maximal as

soon as it leaves the extreme lateral position to become minimal as it reaches the following lateral position (Fig. 6). As the fin crosses the axis of progression, the angle of attack averages 32.4° for five specimens (deleting values in second half of sequences A and C) and ranged from $20-60^\circ$. The average angle of attack value was 29.2° for all caudal fin positions and attained values as high as 100° .

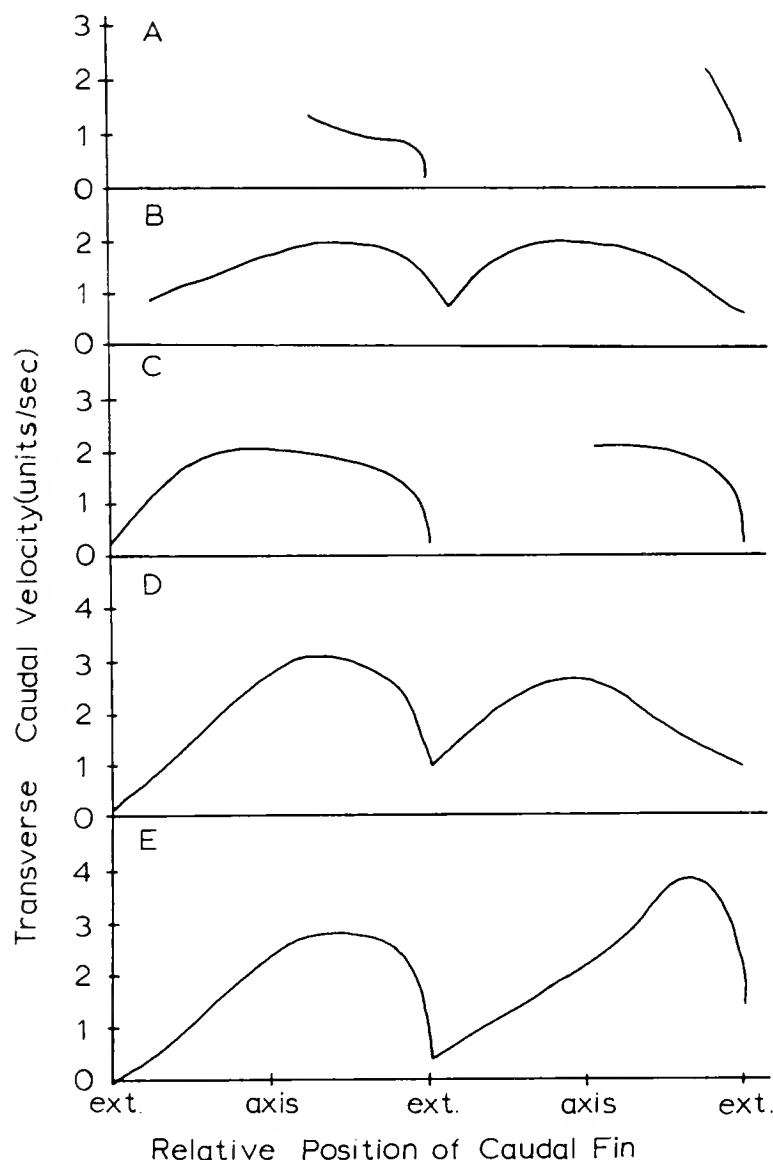


Figure 5. Comparison of transverse caudal velocity with the position of the fin for five sequences of swimming wavyback skipjack. One complete cycle (two sweeps across the axis of progression) is shown for each sequence. Sequences A and C are discontinuous because fin position could not be accurately located in certain of the ciné frames. Letters identifying each sequence correspond to sequences and velocities in Fig. 4.

ext. (LATERAL EXTREME OF CAUDAL SWEEP)
axis (AXIS OF PROGRESSION)

The chord length of the fish never equalled the total length during swimming because the fish always had part of its body curved (cambered) so that the chord length varied from 85% to 95% of the total length (Fig. 1). In about 75% of 31 measurements, the chord length increased when the fish accelerated and decreased when the fish

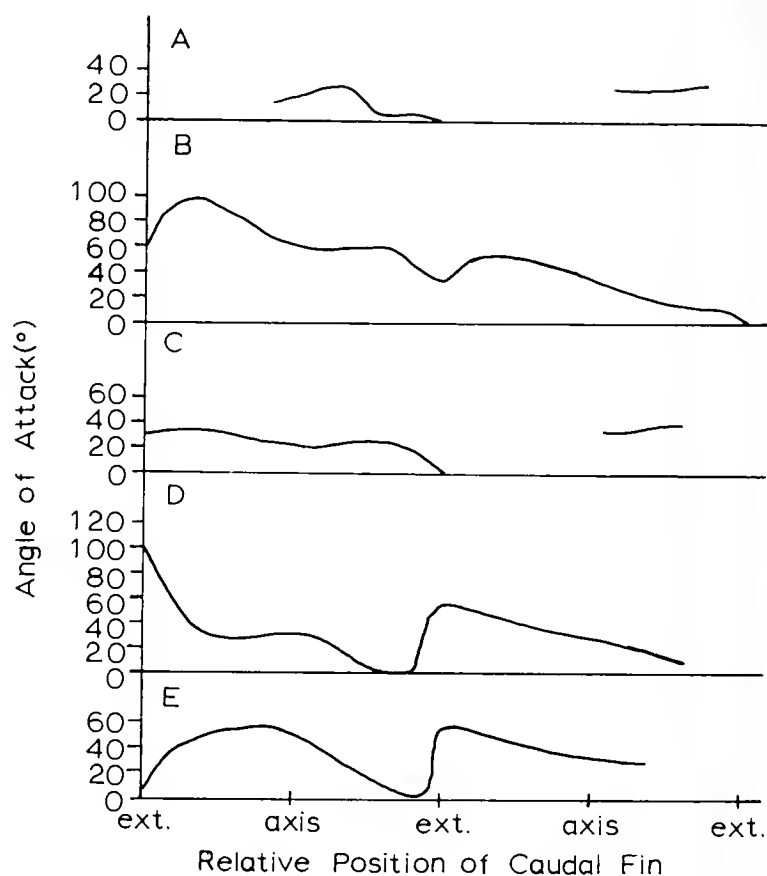


Figure 6. Comparison of angle of attack with the position of the caudal fin for five sequences of wavyback skipjack. Method of measuring angle of attack is given in the text. See explanation of sequences in Fig. 5.

decelerated, however at no time did the chord length shorten during the acceleration phase.

Film strips of Pacific bonito, yellowfin tuna, skipjack tuna and frigate mackerel, although not of the quality to undergo the analysis given here for the wavyback skipjack, definitely suggest that they all swim with movements similar to the wavyback skipjack.

Ciné films of Pacific bonito and wavyback skipjack show that the distal tips of the dorsal and ventral caudal lobes lag behind the proximal or peduncular portions during lateral movement. After the fin has reached its extreme lateral position, the peduncular portion of the fin begins to sweep in the opposite direction before the direction of movement of the distal tips of the lobes is reversed. (Fig. 7).

Thrust and Caudal Fin Movement

The caudal fin-ray amputations performed on two specimens of yellowfin tuna indicate that the caudal rays contribute about 90% of the forward thrust in swimming. The fish with intact caudal rays pulled very strongly upon the hand-line. The fish with amputated caudal rays hardly pulled upon the hand-line even though they appeared to make normal swimming movements. The amplitude and frequency of the movements did not appear to be abnormal. The remaining thrust

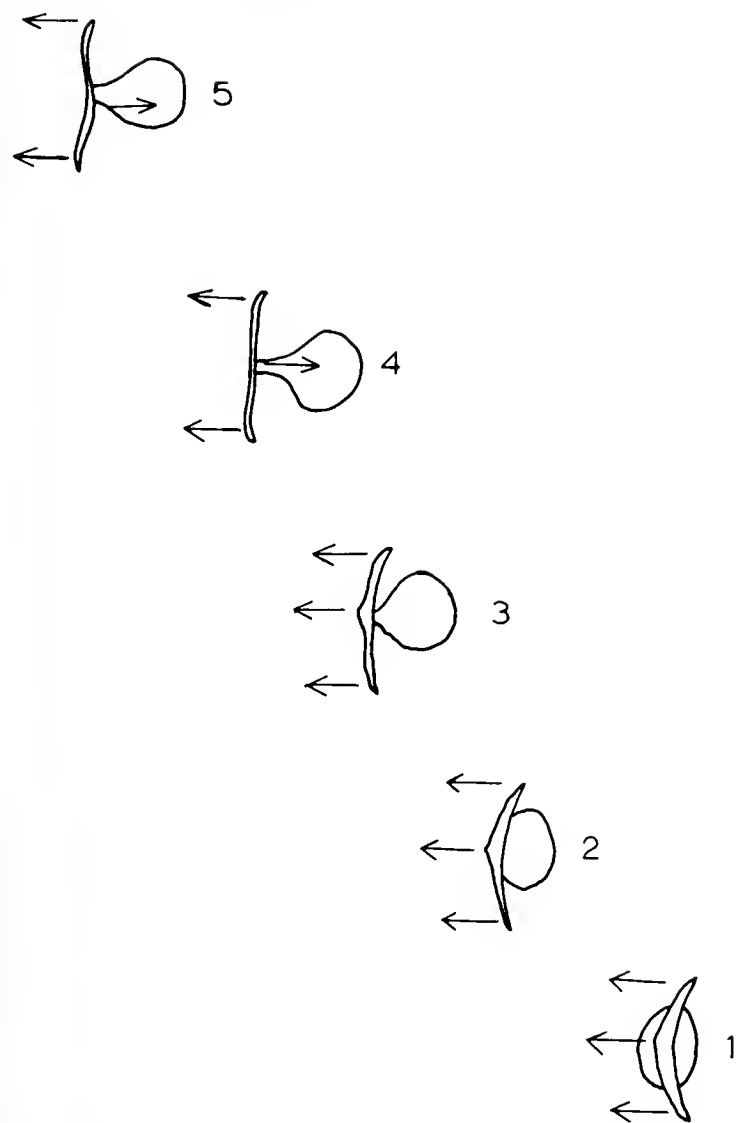


Figure 7. Five successive positions of the caudal fin of the wavyback skipjack seen in posterior view. A semi-diagrammatic illustration based on ciné recording. Note that the fin lobes lag behind the peduncle when the fin reverses direction. Arrows indicate direction of movement. Numbers indicate successive frames (camera speed, 100 frames per sec).

(10%) probably was derived from the fin ray bases and the hypural supports which were not amputated.

The caudal movement studies on freshly killed sierra, yellowfin tuna, skipjack tuna, black skipjack, frigate mackerel, and wahoo showed that as the peduncle oscillated from side to side, the caudal fin always remained parallel to the long axis of the fish. In other words, the angle of attack of the oscillating caudal fin in air is close to 90° when the fish is stationary, but drops to almost 0° when the fish is moved forward through the air. The lateral movement of the caudal fin was executed through two main axial joints, which corresponded to the pre-peduncular and post-peduncular joints seen in the film tracing analysis of wavyback skipjack.

Aspect Ratio

The aspect ratios (AR) of the caudal fins of 15

species of scombroid fishes were measured and the values are listed in descending order (Table 4). The caudal fin AR values were plotted against the fork length for a series of specimens of yellowfin tuna and skipjack tuna (Fig. 8). No change in AR was discerned over the size range of 481-639 mm (skipjack tuna) and 541-934 mm (yellowfin tuna).

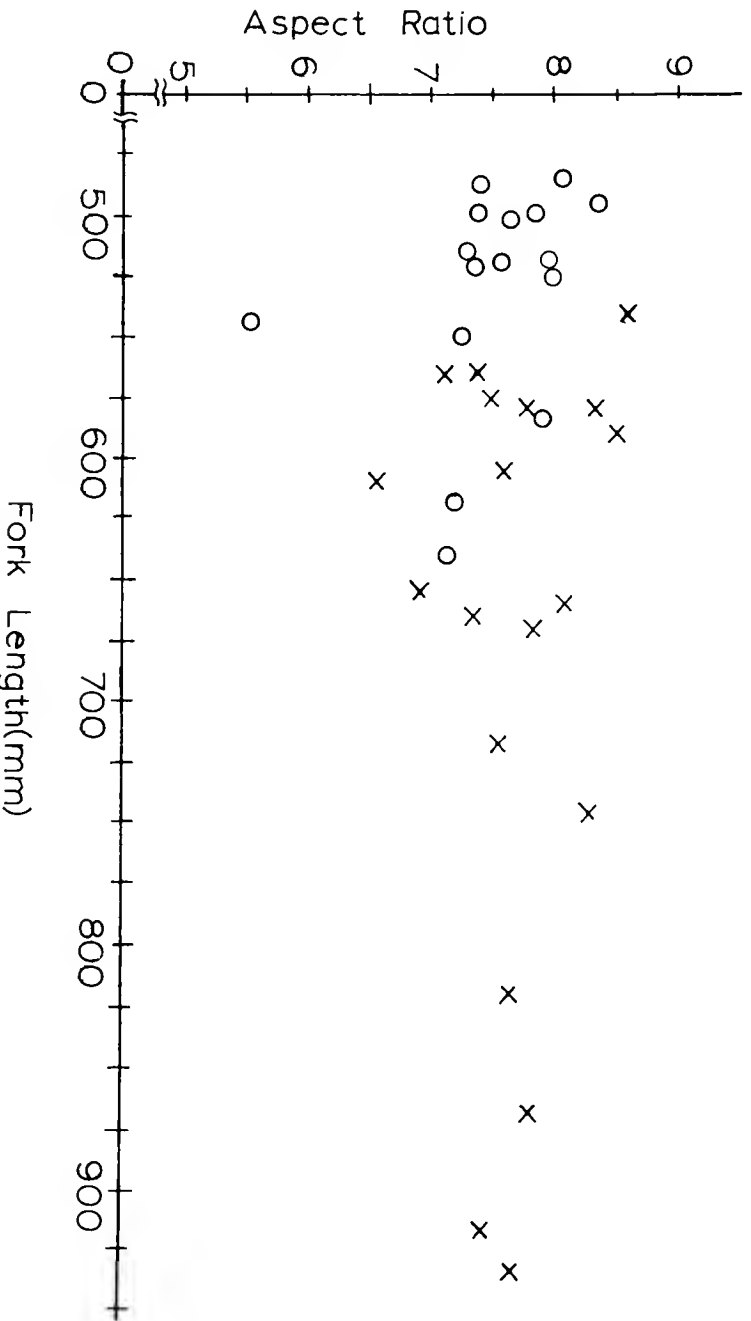


Figure 8. Relationship between aspect ratio of the caudal fin and body size in skipjack tuna (indicated by open circles), and yellowfin tuna (indicated by x's). Fork length defined in text.

Scombroid fishes vary in their ability to alter the span of the caudal fin. The AR of the relaxed caudal fin of five Pacific mackerel (Table 4) averaged 48.7% of the AR of the expanded position which is listed in Table 4. The differences between the span of the expanded and relaxed caudal fins of other scombroids was less noticeable than in the Pacific mackerel. The span of the relaxed

caudal fin of one yellowfin tuna was 66.5% of the expanded position and this change in span seemed to be typical for other large scombrids. In the istiophorids, no change in span was observed, so that the fin structurally was always at maximum expansion. However, the caudal span of the white marlin shrank 4.83 cm a few hours after capture.

TABLE 4. Aspect Ratios of Scombroid Caudal Fins

SPECIES	NUMBER OF SPECIMENS	TOTAL LENGTH (MM)	AR RANGE	MEAN AR
Pacific Sailfish	1	2840	10.26	—
White Marlin	1	2106	9.97	—
Striped Marlin	3	? -3245	7.86-10.11	8.99
Yellowfin Tuna	19	541-982	6.60- 8.70	7.69
Skipjack Tuna	16	481-679	5.53- 8.36	7.49
Black Skipjack	7	315-670	6.74- 7.40	7.06
Frigate Mackerel	7	358-436	6.46- 7.29	7.00
Albacore	7	659-850	6.22- 7.63	6.84
Sierra	5	475-735	5.71- 7.01	6.62
Wahoo	4	1015-1184	5.76- 6.62	6.30
Bluefin Tuna	1	1030	6.01	—
Pacific Bonito	12	440-789	4.81- 6.63	5.71
Swordfish	2	2927-3125	4.19- 6.63	5.41
Pacific Mackerel	7	258-375	4.45- 5.77	5.18
Slender Tuna	1	776	4.69	—

Osteology

The following treatment describes only those features of the vertebral column and caudal fin that are related to normal swimming movements. All descriptions refer to the Scombridae, unless otherwise noted.

Vertebral counts for the various scombroid species are listed in Table 5. All counts were made by the writer except that the range of values for the wahoo was taken from Collette and Gibbs (1962).

TABLE 5. Vertebral Counts for Various Scombroid Fishes

SPECIES	TOTAL NUMBER OF VERTEBRAE
Louvar	22
Pacific sailfish	24
Striped marlin	24
Swordfish	26
Pacific mackerel	31
Escolar	32
Black skipjack	36-38
Wavyback skipjack	39
Yellowfin tuna	39
Frigate mackerel	39
Slender tuna	39
Skipjack tuna	40-41
Pacific bonito	44-46
Sierra	47-49
Wahoo	54-66

The general shape of the vertebrae is characteristic for each family. A typical scombrid verte-

bra has a lateral bony ridge with deep fossae both dorsal and ventral to it (Fig. 9). The istiophorids have elongate, hour-glass shaped centra (Fig. 10A); the xiphiids have short, smooth centra (Fig. 10B); and the escolar is characterized by very light-weight centra which are sculptured with a fine latticework of ridges and grooves.

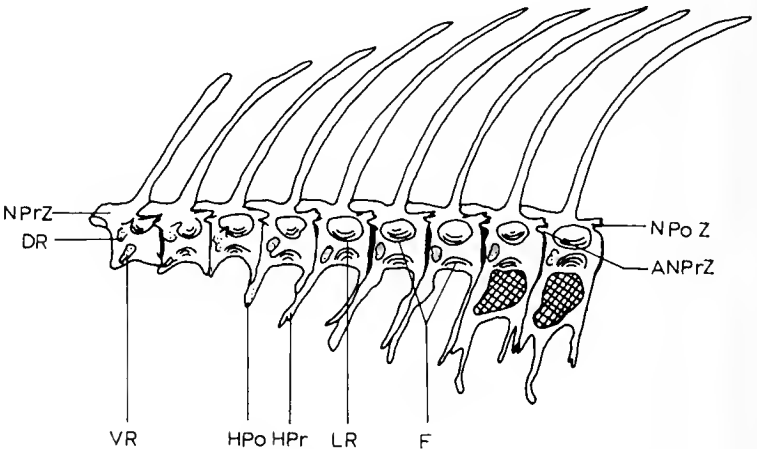


Figure 9. Anterior and posterior abdominal vertebrae of skipjack tuna. Specimen number 630326-02. Rib depressions indicated by stippling and large foramina indicated by cross-hatching.

ANPrZ accessory neural pre-zygapophysis
DR dorsal rib depression
F fossa
HPo haemal post-zygapophysis
HPr haemal pre-zygapophysis
LR lateral bony ridge
NPoZ neural post-zygapophysis
NPrZ neural pre-zygapophysis
VR ventral rib depression

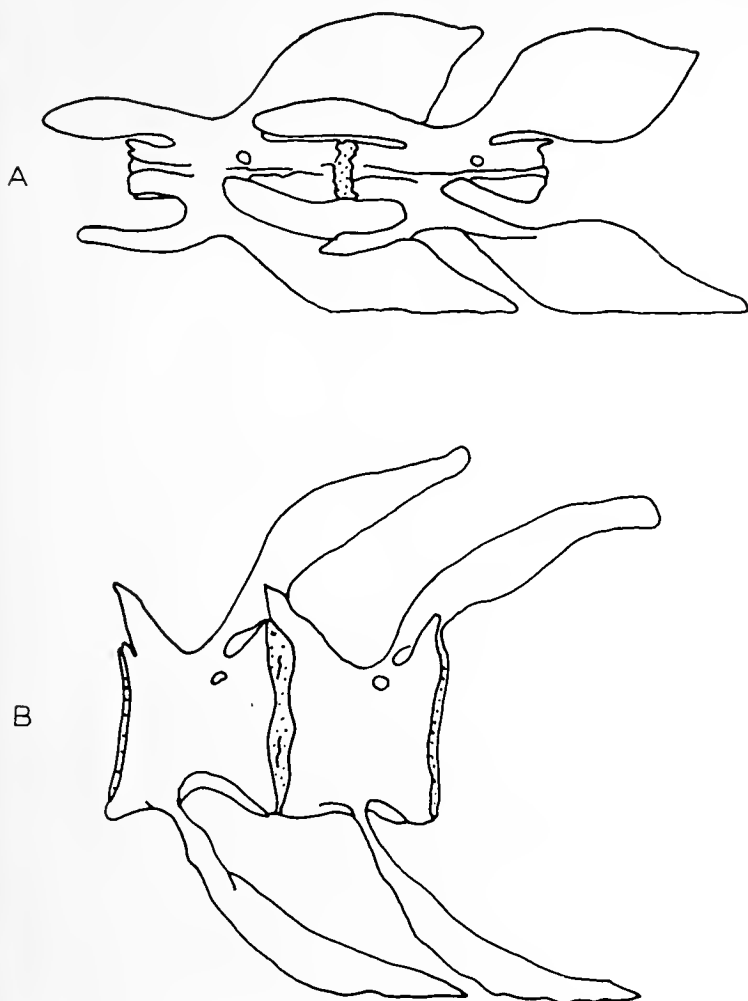


Figure 10. Xiphioid vertebrae.

A. *Istiophorus* Stipple indicates cartilage.

B. *Xiphias* (After Gregory and Conrad, 1937).

Post-Cranial Region

Except for the rounded neural spines of the Pacific mackerel, compressed neural spines are characteristic of this region. The first centrum is attached to the skull and the first neural arch is autonomous (fused to the centrum in the Pacific mackerel). The neural arches are antero-posteriorly elongated to form a bony roof for the spinal cord. In the skipjack tuna, frigate mackerel, black skipjack, and wavyback skipjack, the vertebral canal is divided by a horizontal bony shelf which separates the spinal cord from the more dorsal longitudinal spinal ligament. The neural pre-zygapophyses are large and wedge-shaped and form broad articulations with the next anterior neural arch and the smaller neural post-zygapophyses.

Posteriorly the neural zygapophyses gradually diminish in size and shift dorsally while at the same time the hemapophyses gradually appear. There is a cup-shaped dorsal rib depression high on the neural arch of the first vertebra. This depression moves progressively ventro-laterally until on the posterior vertebrae of this region it is on the lateral surface of the centrum and divides into a dorsal and ventral part. The first three or four vertebrae of the skipjack tuna, frigate mack-

erel, black skipjack, and wavyback skipjack have large posteriorly pointing apophyses which serve as attachments for the tendons of the lateral musculature. In yellowfin tuna, these apophyses are greatly enlarged and project laterally to form "transverse processes" on the third through the sixth vertebrae.

The post-cranial vertebrae of the xiphiids and istiophorids differ from those of the scombrids. The laminae of the istiophorid neural spines do not coalesce to form a neural arch and in these animals the spinal cord is not protected by a dorsal bony cover. The first vertebra is broadly articulated to the skull in the swordfish and there is a large ventral projection from the first centrum which articulates with a similar projection from the basioccipital.

Anterior Abdominal Region (Fig. 9)

The neural pre-and post-zygapophyses are characteristically semi-lunar in shape and are well-developed. Small accessory dorsal pre-zygapophyses develop below the true dorsal pre-zygapophyses to form a depression for the reception of the dorsal post-zygapophysis. The hemapophyses are well developed and haemal post-zygapophyses oppose the hemapophyses. The dorsal rib depression is positioned on the anterior edge of the mid-lateral ridge of the vertebra. The ventral rib depression is located at the tip of the hemapophysis. In the wavyback skipjack, black skipjack, and the frigate mackerel, the hemapophyses of each side fuse together to form a pedicle (Starks, 1910).

Posterior Abdominal Region (Fig. 9)

This region is characterized by haemal arches and in some cases by short haemal spines and haemal pre-zygapophyses. The fossae are well developed (except the Pacific mackerel) on all the centra to give a T-shaped cross section. A short apophysis develops just anterior to the dorsal rib depression of the yellowfin tuna, frigate mackerel, black skipjack, wavyback skipjack, and skipjack tuna. This acts as a support for the laterally projecting dorsal rib. The haemal spines of the skipjack tuna, wavyback skipjack, and black skipjack develop an interconnecting latticework, whereas the hemapophyses of the frigate mackerel develop a long pedicle. In both cases, the haemal post-zygapophyses are elongated and are involved in the latticework as well as in broad intervertebral articulations.

The abdominal vertebrae of xiphiids and istio-

phorids are not divisible into anterior and posterior regions. In the xiphiids, the zygapophyses of adjacent vertebrae do not articulate with each other, whereas the istiophorids have long pre- and post-zygapophyses which articulate with the large plate-like neural and haemal spines.

Anterior Caudal Region

Elongated haemal spines are characteristic of the anterior caudal region. The haemal spines in the anterior part of this vertebral region change anterior to the neural spines to a position directly ventral to the neural spines. In the posterior half of this region, the neural and haemal spines gradually migrate together posteriorly, gradually shorten, and gradually become directed more posteriorly. All the intervertebral zygapophyses gradually become reduced until they are nearly absent between the last two vertebrae of this region. In skipjack tuna, wavyback skipjack, black skipjack, and frigate mackerel, an apophysis develops on the postero-lateral half of the mid-lateral ridge of each centrum. In the frigate mackerel this new posterior apophysis articulates with the anterior apophysis of the next posterior centrum, but posteriorly, the anterior apophysis gradually disappears.

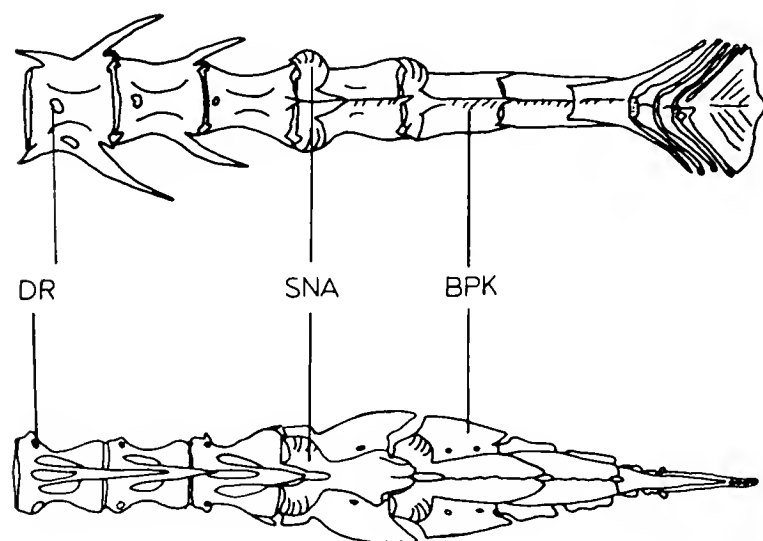


Figure 11. Posterior caudal, peduncular, and caudal fin complex vertebrae of black skipjack. A. Lateral view. B. Dorsal view. Specimen S471, see Table 2 for data.

BPK bony peduncular keel
DR dorsal rib depression
SNA swollen neural arch of first
 peduncular vertebra

Peduncular Region (Fig. 11)

The peduncular region is characterized by depressed neural and haemal spines which overlap succeeding posterior vertebrae. The neural and haemal zygapophyses are much reduced. In the

wahoo, sierra, and Pacific mackerel, the neural and haemal spines assume a horizontal position, but the spines themselves are not flattened. Those scombrids with a depressed peduncle have a bony peduncular keel which develops from the lateral apophyses. The peduncle of the Pacific mackerel has a low ridge similar to a bony keel. The last neural and haemal spines (except the Pacific mackerel) depart from the horizontal and project into the caudal fin. The distal tips of these spines are pointed.

In those species with a bony peduncular keel, the peduncle is in dorsal aspect elliptical with the keel being widest in the middle of the peduncle. The black skipjack has swollen neural and haemal arch bases (Figs. 11 & 22) on the first and second peduncular vertebrae (Godsil, 1954). The peduncular region of istiophorids and xiphiids is short and lacks the dorso-ventral flattening and the bony peduncular keels.

Caudal Fin Complex

This region always includes the last three vertebrae in all scombrids (Fig. 12). The first two vertebrae of this complex are short, have very reduced zygapophyses and they also have neural and haemal spines that project into the caudal fin. The tips of the spines are cup-shaped for the reception of an articular cartilage cap. The haemal spines may or may not be fused with the centrum.

The last vertebra (urostyle) is highly modified and is associated with a number of autonomous elements. Ventrally it articulates with hypural 1 (Gosline, 1961a) which has a large lateral flange (=hypurapophysis of Nursall, 1963b). The distal tip of hypural 1 is cup-shaped. In the Pacific mackerel, two large compressed hypurals articulate with each other as well as with the urostylar centrum. A deep notch separates the two hypurals posteriorly. In other scombrids, the notch may be present (wahoo, sierra) or absent (Pacific bonito, skipjacks, yellowfin tuna, slender tuna, and frigate mackerel), but the hypurals and urostyle are always fused into a single structure, the hypural plate in adult fishes. All scombrids have two epurals, a large epural 1 above the penultimate vertebra and a smaller epural 2 above the urostylar centrum. The urostylar centrum is turned up at its tip and this may represent a fusion of the uroneural and dorsal-most hypural (Ahlstrom, *in litt.*). These elements are not fused in the wahoo. The uroneural may be either completely autonomous (sierra and wahoo) or it may be free from

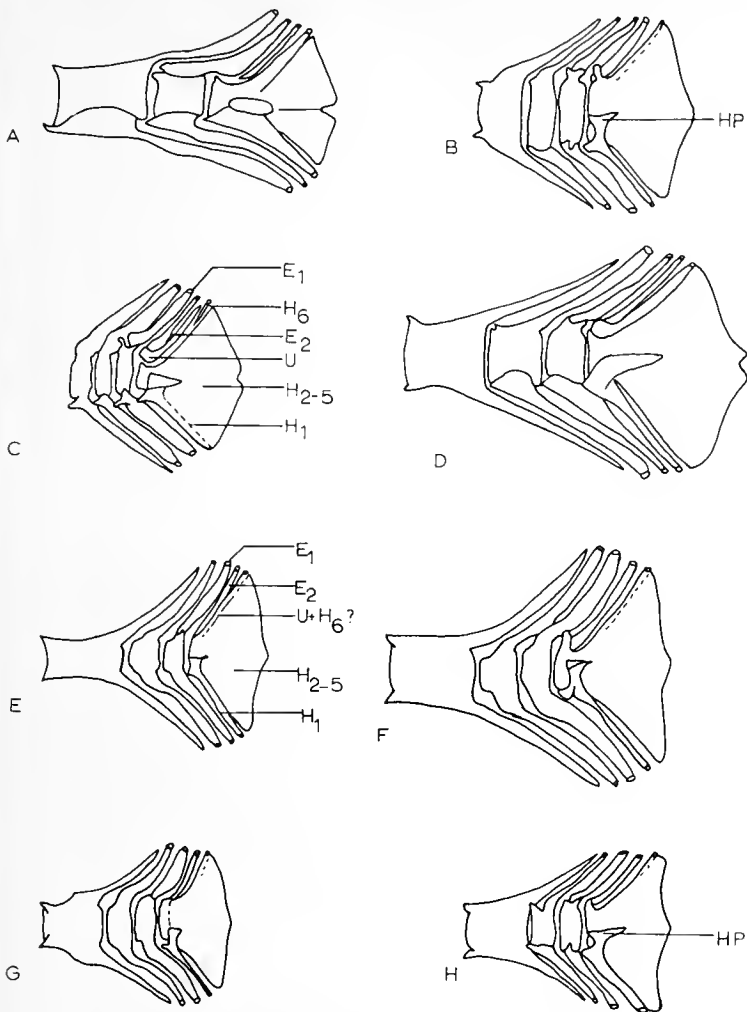


Figure 12. Caudal fin complex of scombrids.

- | | |
|---------------------|-------------------------------|
| A. Pacific mackerel | G. black skipjack |
| B. Pacific bonito | H. yellowfin tuna |
| C. wahoo | E ₁₋₂ epurals 1-2 |
| D. sierra | H ₁₋₆ hypurals 1-6 |
| E. frigate mackerel | HP hypurapophysis |
| F. skipjack tuna | U uroneural |

the hypural plate but fused to the urostylar centrum (Pacific mackerel), or it may be partially fused to the hypural plate and urostylar centrum (yellowfin tuna, Pacific bonito, black skipjack, frigate mackerel, and skipjack tuna). The entire distal border of the hypural plate has a depression for articular cartilage. The hypural plate has ridges and grooves which indicate the positions of the caudal fin ray bases.

The istiophorids and xiphiids have only two vertebrae in the caudal fin complex region (Fig. 13). In the istiophorids, hypural 1 is fused to the other hypurals as well as the urostylar centrum and the hypurapophysis is a large lateral flange. A posterior hypural notch is present and there are three epurals, a large anterior one attached to the penultimate vertebra followed by two smaller epurals. Between the hypural plate and the epurals is a large autonomous anterior uroneural and a small autonomous hypural.

The escolar has three vertebrae in the caudal fin complex region and there is a hypural plate with a posterior notch. There is only one epural and a

uroneural is fused to the urostylar centrum and hypural plate.

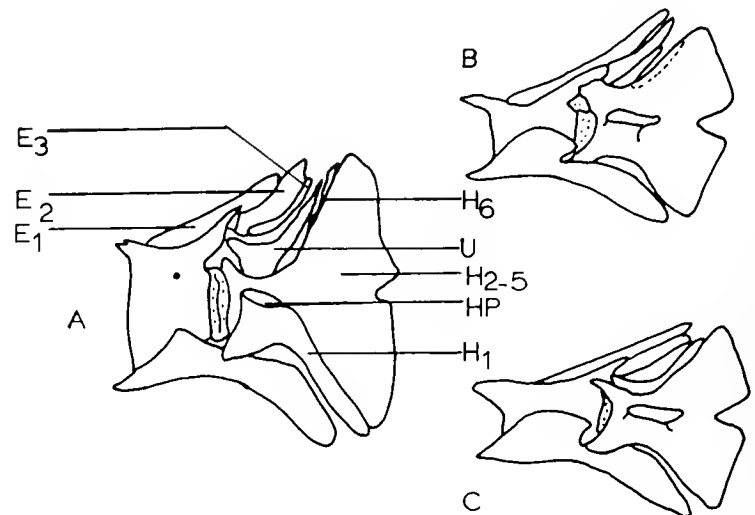


Figure 13. Caudal fin complex of istiophorids and a xiphiid. Abbreviations same as Fig. 15 except there are three epurals (E₁₋₃). (After Gregory and Conrad, 1937).

A. *Xiphias*

B. *Tetrapurus*

C. *Istiophorus*

Caudal Fin

The total number of caudal rays varies from species to species, but the number of principal caudal rays is almost always 17, with nine above the posterior hypural notch and eight below the notch (Fig. 14).



Figure 14. Photograph of caudal fin preparation of yellowfin tuna. Note the overlap of the fin rays upon the hypural plate.

Each ray consists of a right and a left demiray which are bound together by connective tissue and fine muscle fibers for most of the length of the ray; the demiray pairs are fused distally, and proximally they are separated by the hypural plate. All of the principal rays articulate with the hypural plate through a single, common synovial joint (Fig. 15). A continuous band of articular

cartilage within the forks of the principal rays articulates with the articular cartilage caps on each supporting hypural or epural element. The synovial cavity extends slightly onto the lateral surface of the hypural plate.

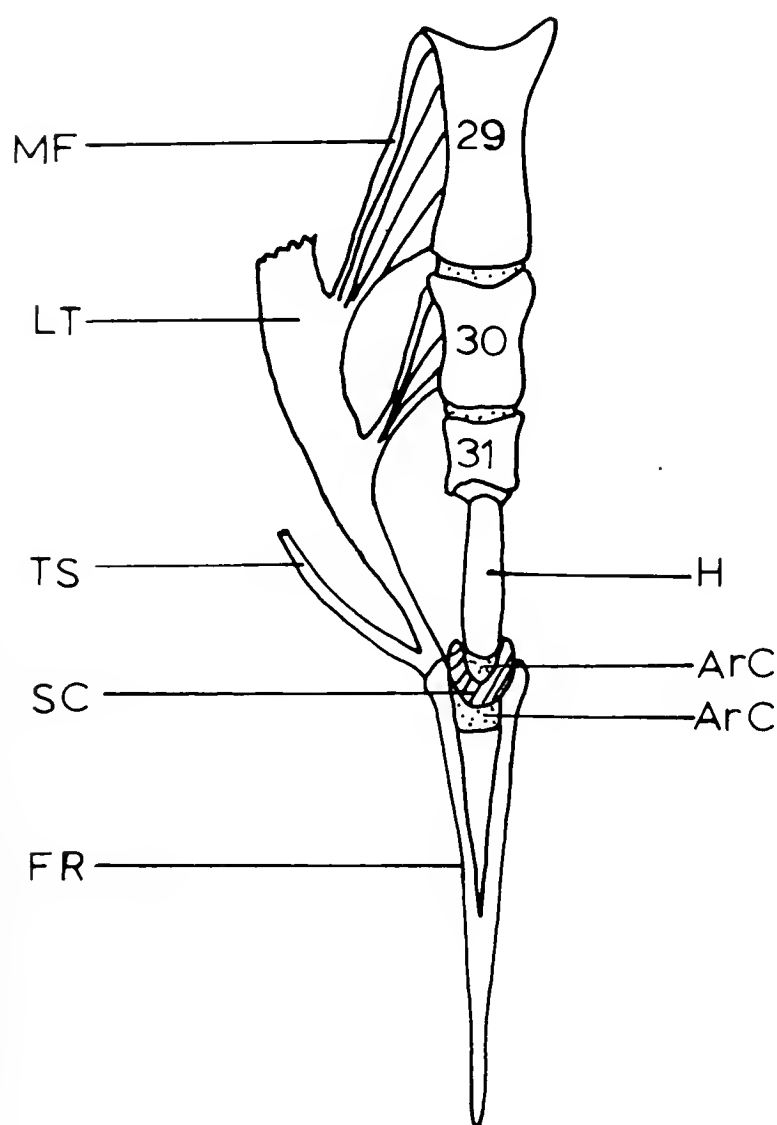


Figure 15. Diagrammatic mid-frontal section through the caudal region of the Pacific mackerel. The contributions of the posterior myomeres to the lateral tendons are shown. Numbers indicate position of vertebrae in vertebral column.

ArC	articular cartilage
FR	middle posterior fin ray
H	hypural
LT	lateral tendon
MF	muscle fibers
SC	synovial cavity
TS	tendon to the skin

With the exception of the middle posterior rays, the caudal rays of all scombroids are closely approximated to each other, and adjacent rays form elongate hinge joints. The posterior surface of each ray is slightly convex to fit into a slightly concave surface of the adjacent posterior fin ray.

On the lateral surface of each fin ray there is a slight eminence (Fig. 14). This is located proximal to the synovial joint on the procurent caudal rays and distal to the synovial joint on the princi-

pal caudal rays. The middle caudal rays which articulate with the posterior edge of the hypural plate have non-overlapping bases and the eminence is positioned just distal to the caudal ray-hypural joint.

A portion of the hypural plate is not covered by the bases of the caudal fin rays. The vertical distance of this bare area, in scombrids, varies from one to three widths of the first principal dorsal caudal ray. In the escolar the space is eight widths wide, in the swordfish it is four widths wide, and in the istiophorid the space is one ray wide. The greatest amount of hypural overlap is exhibited by the first principal ray of each caudal lobe.

The vertebral length gradients were calculated for several species of scombroids. In general the lengths of successive centra gradually increase caudad, and the longest centrum is located near the first penduncular vertebra. The centra posterior to the longest centrum become progressively shorter with the penultimate centrum being the shortest. The curves for most species show a plateau of equal centrum lengths in the middle of the vertebral column; the black skipjack and the Pacific bonito lack this plateau. A very short peduncular vertebra is peculiar to the frigate mackerel.

Myology

The lateral musculature of scombrid fishes comprises 56% (1.47 kg and 451 mm fork length black skipjack and .8 - 1.2 kg Pacific bonito), 64% (5.7 kg and 657 mm fork length yellowfin tuna), and 68% (5.2 and 610 mm fork length skipjack tuna) of the total body weight. There is one myomere per vertebra and superficially each myomere is Σ -shaped (Fig. 16). Deeper dissection reveals that the myomeres are three-dimensional, hollow, complexly folded cones and that the horizontal skeletogenous septum bisects the myomeres into epaxial and hypaxial moieties (Fig. 17). Each moiety is composed of a larger anterior cone (apex directed cephalad) which is adjacent to the horizontal septum and a smaller posterior cone (apex directed caudad) which borders the dorsum of the fish. The muscle fibers of each myomere are more concentrated in the anterior cone than in the posterior cone and muscle fibers run approximately parallel to the long axis of the fish.

The cones of adjacent myomeres are nested, so that in a cross-section of the trunk, the elongated cones appear as groups of concentric rings (Fig. 16). The myomeres in the posterior region of the

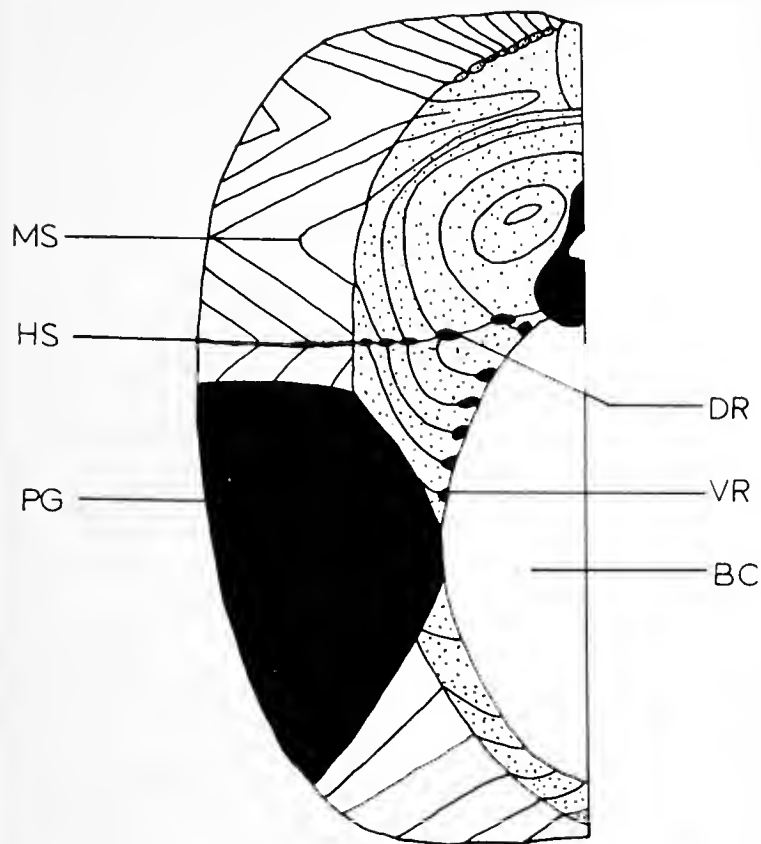


Figure 16. Stereo-diagrammatic view of a cross-section of the trunk of the Pacific bonito. View is from the posterior. It illustrates the relationship of the superficial myomere pattern to the concentric circles of muscular tissue. Cut surface is stippled.

BC body cavity
DR dorsal rib
HS horizontal skeletogenous septum
MS myoseptum
PG pectoral girdle, blackened
VR ventral rib

body are antero-posteriorly elongated and the number of concentric rings seen in cross-section is directly proportional to the degree of myomere elongation. At the level of the anal opening, the Pacific mackerel has three or four, Pacific bonito and wahoo have ten, yellowfin tuna has 13, and skipjack tuna has 17 concentric myomeres. The degree of myomere elongation probably may vary directly with body size because young specimens of an unidentified species of *Auxis* were noted to have six (17 mm total length), eight (45 mm total length), nine (77.5 mm total length), and 11 (110.5 mm total length) concentric rings of myomeres at the level of the anal opening.

Red muscle tissue is concentrated along either side of the horizontal septum (Fig. 17). This tissue is an integral part of each myomere and cannot be separated from the more abundant white muscle fibers. Pacific mackerel, Pacific bonito, sierra and wahoo have superficial red muscle, whereas yellowfin tuna, skipjack tuna, frigate mackerel, and black skipjack have a more deepseated red muscle.

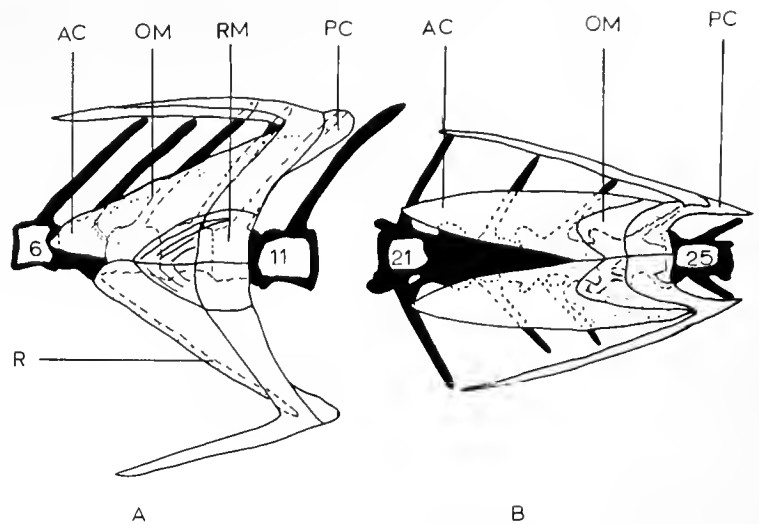


Figure 17. Two individual myomeres from Pacific mackerel. Note relationship with vertebral column. Positions of the vertebrae are indicated by numbers. Exposed vertebrae are blackened.

A anterior myomere PC posterior cone
B posterior myomere R ventral rib
AC anterior cone RM red muscle
OM origin of myomere, indicated by stipples

Each myomere is separated from its neighbors by a connective tissue myoseptum which serves as a common attachment for the muscle fibers of two adjacent myomeres (Fig. 16). Various parts of the myoseptum are thickened to form tendons. A maximal number of three different tendon sets are formed from the myoseptum of the epaxial anterior cone and one set of tendons is formed in the myoseptum of the smaller epaxial posterior cone (Fig. 19). Similarly, the same four tendon sets may be presented in the myoseptum of the hypaxial cones. In the anterior cone, two of the tendon sets insert posteriorly from their myoseptum of origin; one tendon set is deep and the other set is superficial.

The deep tendon set forms the posterior oblique tendons described by Kafuku (1950). These originate from connective tissue fibers of the myosepta of the epaxial and hypaxial anterior cones to extend posteriorly in the horizontal septum (Figs. 18, 19). The posterior oblique fibers of the epaxial and hypaxial cones are fused so that there is only one posterior oblique tendon per vertebra in all scombrids. In the Pacific mackerel, the posterior oblique tendons cross approximately three intervertebral joints before inserting on a vertebra (Kafuku, 1950), whereas in the skipjack tuna, these tendons cross approximately seven intervertebral joints (Fig. 18). The red muscle part of each myomere is adjacent to the posterior oblique tendons (Fig. 18). A short, flat dorsal rib articulates with each centrum within the horizontal septum just anterior to the vertebral attachment of each tendon. For all scombrid species, the first

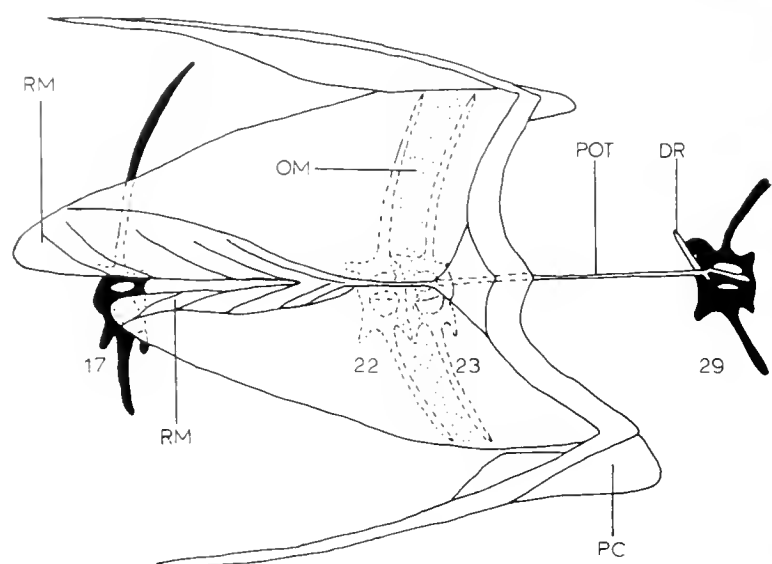


Figure 18. A single myomere from the mid-trunk of a skipjack tuna. Note its relationship to the vertebral column. Numbers indicate position of vertebrae in vertebral column.

- DR dorsal rib
OM origin of myomere, indicated by stipple
PC posterior cone
POT posterior oblique tendon
RM red muscle in anterior cone

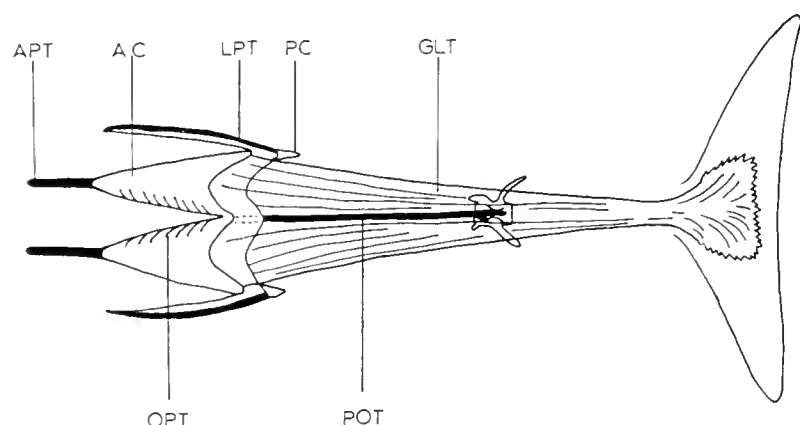


Figure 19. Summary diagram of a composite scombrid myomere and its tendons. Explanation in text.

- AC anterior cone
APT anterior projecting tendon
GLT great lateral tendon
LPT lateral projecting tendons
OPT origin of posterior oblique tendon
PC posterior cone
POT posterior oblique tendon

peduncular vertebra provides the most posterior attachment for the posterior oblique tendons.

The superficial tendon sets of the epaxial and hypaxial anterior cones unite to form a great lateral tendon (Figs. 20, 21). A cross-section through this tendon shows that it consists of nested cones which represent contributions from the various myosepta and in this manner is quite unlike a solid mammalian tendon. This great lateral tendon courses past the peduncle to insert upon the caudal fin rays.



Figure 20. Superficial dissection of a black skipjack. Note the great lateral tendon bypassing the peduncular region and inserting onto the caudal rays. Skin with fleshy peduncular keel is reflected.



Figure 21. An intermediate caudal dissection of a black skipjack. Note an intermediate set of lateral tendons which insert onto the caudal fin rays. Same specimen as Fig. 20. Skin with fleshy peduncular keel is reflected. The posterior portion of the great lateral tendon is cut and reflected dorsally.

The third tendon set of the anterior cone is found in the anterior region of the body of the frigate mackerel (Fig. 19). The apices of the anterior cones of the myosepta are thickened to form a continuous tendon which inserts on the pectoral girdle. This tendon set was not noticed in other scombrids. Kishinouye (1923) was the first to describe and illustrate this tendon set.

Throughout the length of the body, the superficial edge of each myoseptum, which contributes to the dorsal part of the posterior cones, is thickened into a weak tendon (Fig. 19). These small tendons each unite laterally with the superficial (subcutaneous) fascia which surrounds the lateral musculature.

The anterior cones lose their vertebral attachments at the level of the first peduncular vertebra (Fig. 22). The smaller posterior cones continue to attach to the vertebrae in the peduncular region and become covered laterally by the anterior cones which have assumed a more superficial

position. The anterior cones at this point have lost nearly all muscle fibers and are almost completely tendinous. In scombrids having a bony peduncular keel (yellowfin tuna, Pacific bonito, skipjack tuna, wavyback skipjack, and frigate mackerel), the lateral tendons follow the contour of the lateral edge of the bony peduncular keel rather than coursing next to the peduncular centra to enter the caudal fin. This leaves the peduncular centra and the dorsal and ventral surfaces of the keel (if a keel is present) for the insertion of the posterior cones.

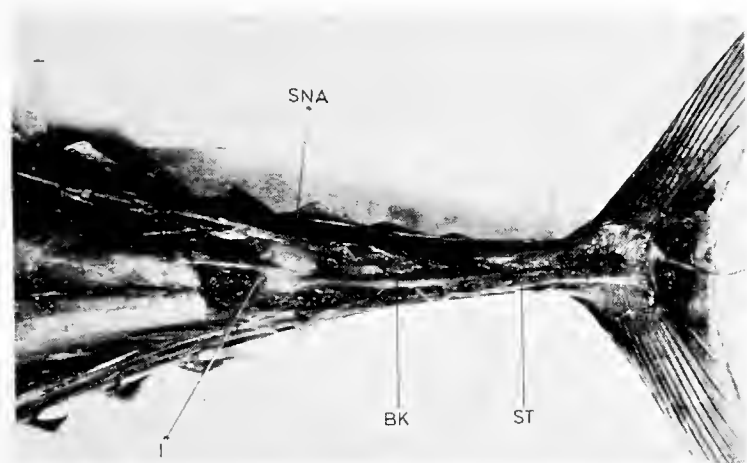


Figure 22. A deep caudal dissection of a black skipjack. Note a small set of tendons which insert onto the posterior middle caudal rays. The dorsal small tendon is reflected, whereas the ventral small tendon is in place. Same specimen as Fig. 20.

- BK bony peduncular keel
- SNA swelling of neural arch on first peduncular vertebra
- ST ventral small tendon
- I posterior-most insertion of lateral musculature before bypassing peduncle

After entering the caudal fin complex, the great lateral tendons unite into a common aponeurosis which fans out and inserts upon each principal caudal ray (Figs. 15, 20). These aponeurotic insertions are located on eminences which lie just distal to the caudal ray hypural joints. Upon deeper dissection (Fig. 21), a set of smaller lateral tendons from the anterior cones of the posterior myomeres is seen to insert by an aponeurosis upon all except the middle caudal rays. Still deeper dissection (Fig. 22) reveals a third smaller set of tendons which inserts upon the middle caudal rays. The origin of this small set of tendons varies from species to species. In the Pacific mackerel these smaller tendons originate only from the posterior cones. In the yellowfin tuna they originate from both the middle set of tendons and the posterior cones which fill the peduncular region, whereas in the black skipjack these small

tendons only originate from the medial side of the middle set of tendons.

In the Pacific mackerel, yellowfin tuna, and Pacific bonito a large tendon spans the distance between the hypurapophysis and the first dorsal principal caudal ray. In addition, these three species have a muscular band that runs from the ventral border of the hypurapophysis to the ventral-most middle caudal ray. Only the Pacific mackerel has a ventral tendon that runs from the hypurapophysis to the first ventral principal caudal ray. In the black skipjack there is no intrinsic caudal musculature.

The interradiialis muscle is well-developed in all scombrids.

The myology of the trichiurids, istiophorids, and xiphiids differ from the myology of the scombrids. These fish lack the stout lateral tendons and the elongated myomeres, and they have well-developed intrinsic caudal musculature (Figs. 23, 24, 25). The myomeres of the istiophorids and xiphiids have myoseptal inscriptions and the swordfish has as many as five myosepta per myomere. The stout hypurapophysis of the Istiophoridae provides a strong posterior insertion point for the lateral musculature, which is unlike all other scombrids.

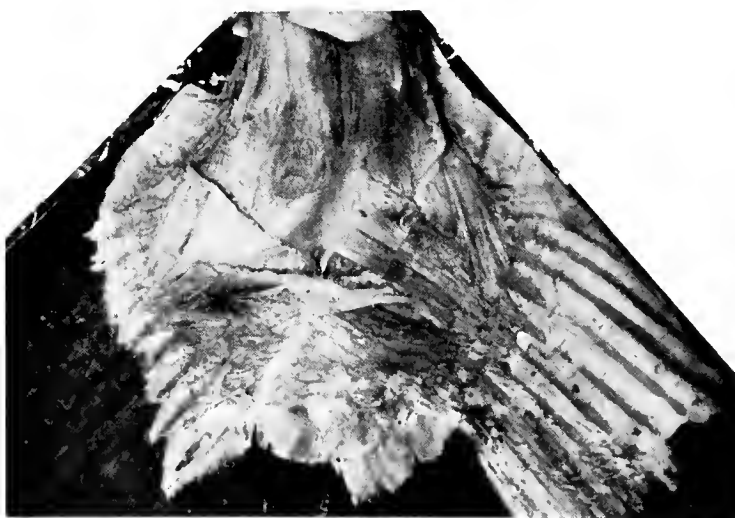


Figure 23. Superficial caudal dissection of a swordfish. Note that the caudal musculature is continuous with the lateral myomeres.

DISCUSSION

Acceleration Rates

The maximum acceleration rates for yellowfin tuna and wahoo (Table 3) are comparable with the values for the trout and the perch (Table 6). An interesting feature is that the scombrids attain high acceleration values at speeds in excess of 19 m/sec. Since drag normally increases with in-

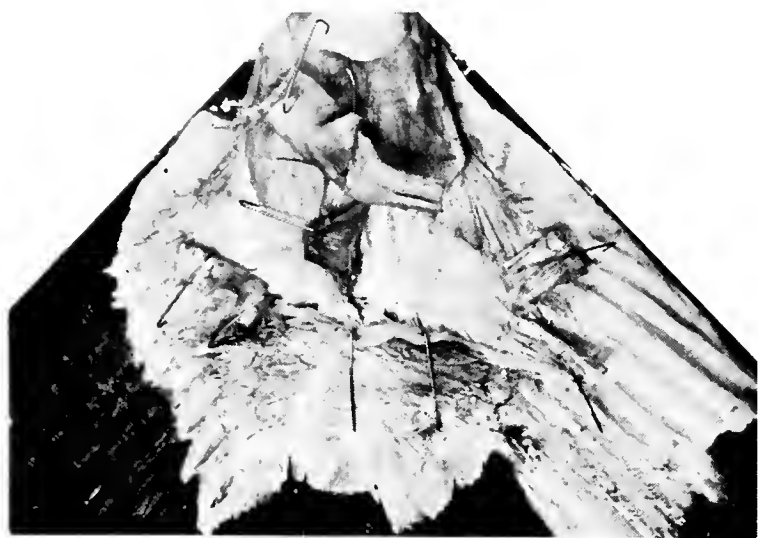


Figure 24. Deep caudal dissection of a swordfish. Note the numerous intrinsic caudal muscles which are reduced in the Scombridae. Same specimen as Fig. 23.

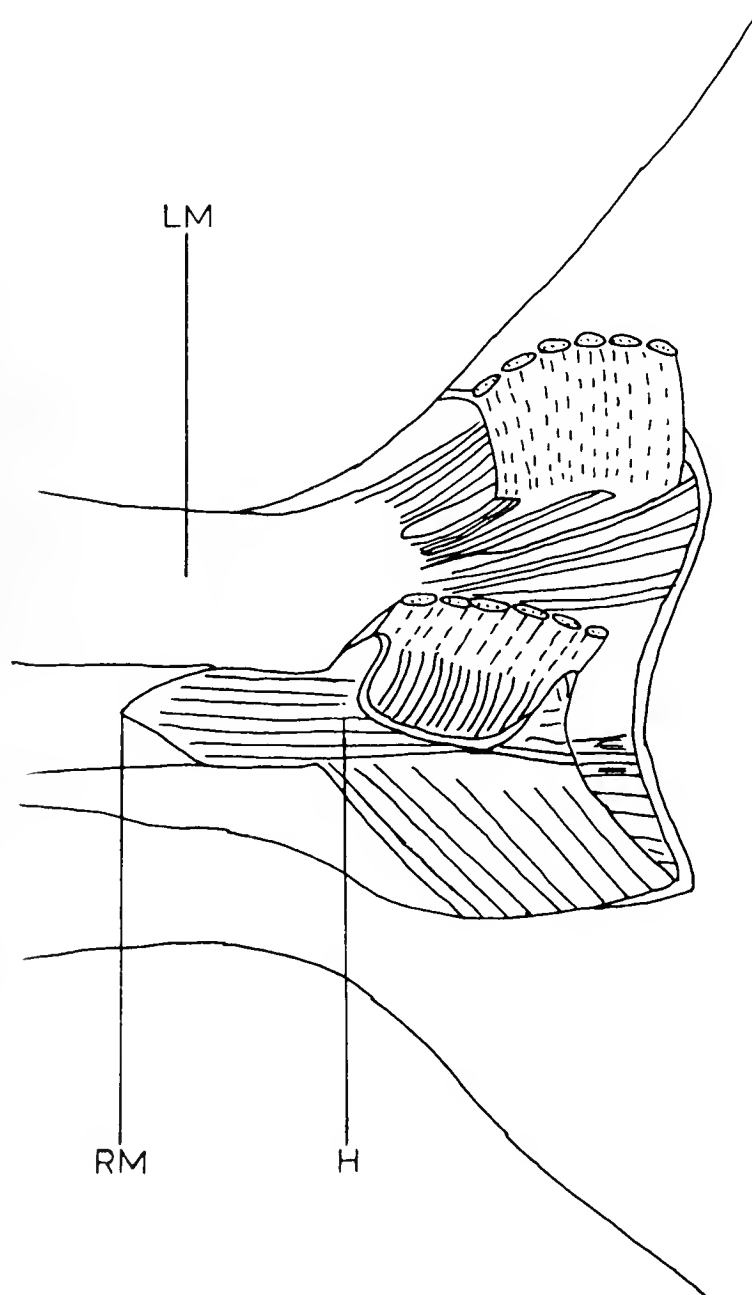


Figure 25. Preliminary caudal dissection of a striped marlin. Note the numerous intrinsic caudal muscles and the insertion of the red muscle (which is not hyper-developed) upon the large hypurapophysis.

H hypurapophysis
LM lateral muscle
RM red muscle

creasing velocity, then the scombrids must experience a drag reduction in order to accelerate at these high velocities at the same rate as the trout and perch did from a standing start. Since the scombrids were attached by a hook and line to the recording apparatus, the line and lure must have decreased the maximum acceleration rate.

Harris (1953) stated that due to the shape of the scombrid caudal fin, the tail would 'stall' with a sudden burst of speed from a standing start. Our data neither support nor refute this conclusion since the acceleration of a yellowfin tuna and a wahoo was never measured from a standing start. The closest value to a standing start is 2 m/sec for yellowfin (Table 3) which accelerated at 37.3 m/sec/sec.

Each oscillogram consists of peaks of relatively long duration which contain symmetrical lesser pips of short duration (Fig. 3). Nursall (1958a) showed that trout do not swim at a constant rate in a trough of running water, but are always adjusting to their environment and the more rapid the alternation of acceleration and deceleration, the more constant would be the speed of the fish. Following this line of reasoning, the smaller pips in the scombrid oscillograms would represent the fish adjusting to their environment (presumably local turbulences), and the broader and larger peaks would represent the fish changing either its speed or its direction of movement with respect to the recording apparatus. However, the swimming performances of the yellowfin tuna and wahoo were recorded in the open ocean, where there is considerably less local turbulence than in a hatchery trough. It is likely that the smaller pips in the scombrid oscillograms reflect head wobble, tail beat, or variations in the transverse caudal velocity.

Swimming Analysis, Thrust and Caudal Fin Movement

Breder's (1926) account of carangiform movement is descriptive of the movements observed in the scombrids. The wavyback skipjack has a body-length:wave-length ratio ($R:\lambda$) greater than 0.5 and less than 1.0. Kramer (1960) stated that the mackerel swims with pendulum movement similar to ostraciiform fish ($R:\lambda = 0.5$) and extrapolated his results to include the tunas. This is in disagreement with our observations on scombrids that they all swim in a manner similar to the wavyback skipjack. The minnows (bream, dace, and goldfish) swim with a $R:\lambda$ of 1.6, 1.7, and 1.4 respectively (Bainbridge, 1963), which indicates they have anguilliform movements.

TABLE 6. Recalculated Acceleration Values for a Trout and a Perch

	LENGTH OF FISH (CM)	DURATION (SEC)	START VELOCITY (CM/SEC)	END VELOCITY (CM/SEC)	ACCELE- RATION (CM/SEC ²)
Trout (Gray, 1953)	22.86	.05	0	223.5	4,470
Perch (Gero, 1952)	—	.0156	0	81.15	5,201.92

According to the data presented by Bainbridge (1963), there is no part of the fish's body that moves along the axis of progression. Minnows (bream, goldfish, dace) have a point of minimum yaw amplitude near the posterior edge of the operculum and the amplitude increases cephalad and caudad from this point, but a node at which the amplitude of movement is zero was never located. The wavyback skipjack has its point of minimum amplitude at the anterior edge of the pectoral fin base, which is close to the vertical, posterior edge of the operculum (Figs. 1, 4). In this respect, scombrid swimming resembles the swimming of minnows.

The mean yaw amplitude at the snout for the wavyback skipjack is about twice that amplitude at the posterior edge of the operculum. This is approximately the same absolute value that Bainbridge (1963) found for the three fresh water fishes. When these values are put in relative terms, then the mean snout amplitude: body length ratio for the five specimens of wavyback skipjack is 0.030, whereas the snout amplitude:body length ratio taken from Bainbridge's data is 0.096 for the goldfish, 0.066 for the bream, and 0.036 for the dace. The relative head length, amount of lateral compression of the head, and the mass of the head relative to the body should influence the amount of lateral movement of the head. The head is approximately one-fourth the total length of the body for wavyback skipjack, goldfish, bream, and dace, but the head is more compressed in the wavyback skipjack and might account for some of the lack of wobble. In addition, most of the mass of scombrids lie in the forward one-half of the body and this would also decrease the yaw at the snout owing to inertia.

Bainbridge (1958) showed for the minnows (goldfish, bream, and dace) that above 5 tail beats/sec the amplitude of tail beat remained constant and that the forward velocity was directly proportional to the tail beat frequency. The five wavyback skipjack (Fig. 4) indicate that the forward velocity varies directly with amplitude (except sequence D) as well as with the number of

tail beats/sec. Thus, above 5 beats/sec the scombrids can still increase the amplitude of the tail beat, whereas the minnows apparently do not do so.

Using Bainbridge's (1963) data, when the amplitude of the caudal tip is expressed in terms of body length, the goldfish had an amplitude .24 times the body length, the bream had a value .23 times the body length, and the dace had a caudal amplitude .27 times its own body length. The relative yaw amplitude for the middle of the caudal fin for the five wavyback skipjacks (Fig. 4) has a maximum value of .30 (sequence E). Thus, the relative yaw amplitude of the caudal fin of scombrids may be relatively greater than the minnows.

Breder (1926) noted that when the caudal fin was removed from *Scardineus erythrophthalmus*, the swimming speed was not impaired because the fish increased its frequency and amplitude of undulation to compensate for the loss of the fin. Gray (1933) confirmed these results when he reported that removal of the caudal fins from the whiting, rudd, and perch did not reduce swimming speed. Gray computed that the caudal fin of the whiting normally contributes 40% of the thrust, but when the fin is amputated, the rest of the body can increase its development of thrust by two-thirds. Bainbridge (1963) mathematically assessed that during normal swimming the caudal fin contributes 45%, 65% and 84% of the total thrust, respectively, for the bream, goldfish and dace. He felt that these differences could be accounted for on the basis of differences in body movement. No attempt was made to see whether this caudal thrust could be transferred to the body if the caudal fin were amputated, although it is likely that it could be so transferred.

The two caudal amputation experiments on yellowfin tuna show that: 1) the caudal fin contributes nearly 100% of the thrust and 2) the fish does not generate any appreciable thrust from other than the caudal fin. Admittedly, these experiments were executed crudely, but they are corroborated by certain Southern California

sports fishermen who use live Pacific mackerel as bait for the yellowtail (*Seriola dorsalis*). If the Pacific mackerel is put on the hook intact, then the fishermen report that they must constantly 'fight' the bait. However, if the caudal fin rays are amputated, the bait will maintain a normal body position, although it is unable to swim with an appreciable forward thrust. Since the Pacific mackerel is regarded as a primitive living scombrid, the emphasis on caudal thrust may have appeared early in scombrid phylogeny.

Nursall (1956) pointed out that the major axis of lateral bending for the entire body of the little tuna (*Euthynnus alleteratus*) appeared to be immediately anterior to the first peduncular vertebra (the thirty-third) and that the caudal fin has its own axis of bending through the small vertebrae supporting the caudal skeleton. Kramer (1960) showed through the use of models that pendulum motion could not be efficient if the caudal fin were rigid and that joints must be developed if a fish is to utilize long wave-length movements. He then pointed out that in terms of swimming movements, the cetaceans (described by Parry, 1949a, 1949b, and Slijper, 1962) and the tunas are similar although the former undulate their bodies in the vertical plane and the latter undulate in the horizontal plane. The films used in the present study give photographic evidence of the dual-joint system proposed by both Nursall (1956) and Kramer (1960)¹.

Bainbridge (1963) has been the only author to describe in detail the changes in shape, position and transverse speed of the caudal fin during the tail beat cycle. Since it was impossible to study fin shape changes in detail with the wavyback skipjack only the measurements of angle of attack and speed of transverse movement of the caudal fin will be compared with Bainbridge's measurements. Bainbridge noted that the caudal speed was zero at the lateral extremes and that the point of maximum transverse velocity was different for each of the three fishes that he studied. For the bream, the maximum transverse velocity was attained about midway between the lateral extreme and the axis of progression, and was maintained across the axis of progression to a point midway between the axis of progression and the opposite lateral extreme, beyond which it diminished to

zero. For the dace, the maximum velocity was at the axis of progression and once the fin passed the axis, it began to decelerate. The goldfish, however, displayed an asymmetrical curve, so that the fin had its highest velocity about one-third of the way between the extreme and the axis of progression and then the speed gradually diminished until it reached the other extreme limit; in other words the fin began to decelerate before it crossed the axis of progression. The five specimens of wavyback skipjack had the highest transverse caudal velocity near or past the axis of progression (Fig. 5). This results in an asymmetrical tail beat which is the reverse of that found in the goldfish.

In the wavyback skipjack the curve plotting the angle of attack versus fin position has a different type of asymmetry from the transverse caudal velocity versus fin position curve (Fig. 9). The angle of attack is highest on the approaching side, decreases as it crosses the axis of progression, and continues to decrease until it reaches a zero value at the opposite extreme from which it started. The average angle of attack value was 29.2° for all observed caudal fin positions and attained values around 100° . Bainbridge (1963) computed mean values of $13\text{--}14^\circ$ for the dace and goldfish and stated that these values are what would be expected if the caudal fin were regarded as an inclined plate, in other words, the efficiency of a rigid airfoil (hydrofoil) is highest with an angle of attack of about 11° (Schlichting, 1960, Fig. 1.12).

However, the oscillating caudal fin of a fish can not be regarded as a rigid inclined plate. Although the hydrodynamics of oscillating hydrofoils is poorly understood (see discussion in Nursall, 1962) it appears that oscillating hydrofoils can operate efficiently at higher angles of attack than can non-oscillating hydrofoils. Indeed, mechanical scombrid models swim faster with attack angles of $20\text{--}25^\circ$ (Kramer, 1960) and wavyback skipjack swim with an average angle of attack of 32.4° as the fin crosses the axis of progression.

While the angle of attack of the wavyback skipjack decreases as the fin sweeps from one lateral extreme to the other, the transverse velocity of the fin increases (Figs. 5, 6). Nursall (1962) states that the angle of attack in the eel is minimal at the axis of progression. This inverse relationship between transverse caudal speed and angle of attack may function to attain a constant thrust (cf. Gero, 1952, Fig. 11). This observation also suggests that the highest angle of attack is possible only during the slower or accelerating phase of the normal transverse caudal cycle and that the

¹According to Carl L. Hubbs (personal communication), isurid galeoid sharks (i.e. porbeagles [*Lamna* sp.], maneaters [*Carcharodon carcharias*], and makos [*Isurus* sp.]) swim like tunas, whereas in the authors' experiences other sharks in open water swim like eels or minnows.

angle of attack drops thereafter until the fin reaches the opposite extreme position. The rate of decrease of the angle of attack is dependent upon many factors: such as velocity of the fin and structural rigidity of the fin.

The observation that the caudal fin of freshly killed scombrids remains parallel to the main body axis as the peduncle oscillates, indicates that the angle of attack is about 90° in air (stationary fish) or about 0° if the fish is mechanically moved forward. This was not observed in the swimming sequences of the wavyback skipjack. Thus, the angle of attack results from the muscular power applied to the caudal fin, from the resistance of the water, and from the structural strength of the fin.

In an airplane wing, the camber and airflow is such that a negative pressure develops above the wing and a positive pressure develops below the wing to create a lift component. A similar comparison to the camber of the fish caudal fin would indicate that the positive pressure develops on the retreating surface and the negative pressure develops on the advancing surface of the oscillating fin. However, this is just opposite to what is truly the case. The advancing surface of the caudal fin creates a positive pressure, and only in this way can a forward vector be produced by the fin. Thus, the camber of the fin is the opposite of that found in the airplane wing.

Bainbridge (1963) showed that the caudal fin leads with its dorsal and ventral tips during a lateral sweep. When the center (hypural base) of the fin reached the lateral extreme, the dorsal and ventral caudal fin tips were already moving back toward the axis of progression. Bainbridge postulated that this phase difference between the tips and the base smoothed out the lateral sweep in order to reduce what would be a loss of forward thrust produced at the lateral extremes when the fin reversed direction. The analyses of the Pacific bonito and wavyback skipjack (Fig. 7) show that the center (hypural base) of the fin leads while the tips of the fin lag behind. Nevertheless, the phase difference between the center and the tips of the fin probably acts to smooth out the caudal thrust. It is most likely that the dihedral of the caudal fin of the Pacific bonito and wavyback skipjack is representative of the dihedrals of the caudal fin of other scombrids.

Since Bainbridge's fish led the caudal sweep with the tips of the fin, one would expect a relatively high positive pressure at the tips and a relatively low pressure at the hypural base. This dihedral would promote water flow towards the

center of the caudal fin (hypural base) from the caudal tips. On the other hand, the scombrid caudal fin's dihedral would promote flow away from the hypural base towards the tips of the caudal fin. This would promote caudal fin tip turbulence. The small fleshy caudal keels which converge caudad in all scombrids are thought to accelerate the flow past the hypural base (Walters, 1962) and thus, a negative pressure would be produced at the hypural base to prevent caudal fin tip turbulence.

Aspect Ratio

The mean AR values (Table 4) are much higher than those values Nursall (1958b) measured for scombrids (6.1 for white marlin to 4.1 for the sierra). Our methods of measuring the AR were compatible (Nursall, *in litt.*), but we measured fresh or frozen specimens, whereas Nursall worked with formalin-fixed material. Since formalin fixation shrinks biological material and since a slight change in the span would change the AR by the second power, then the different states of preservation could account for the discrepancy in AR values as determined by Nursall and by us. Also, fixed fins cannot be spread out as much as fresh fins, even if no shrinkage occurred.

Nursall assumed that an AR of 6.1 was close to the structural limits of the building material, even though he recognized an AR between eight and ten to be hydrodynamically most efficient. In light of our new measurements, AR values between 8 and 10 are found in skipjack tuna, yellowfin tuna, striped and white marlin and Pacific sailfish, but not in the families Scombridae and Cybiidae, following Berg (1940).

The most highly specialized marine mammals (cetaceans) have fluke aspect ratios comparable with caudal fin aspect ratios of highly specialized elasmobranchs (isurid sharks). Neither group has been able to build a hydrofoil which approaches the hydrodynamic efficiencies of the caudal fins of the more specialized scombrid groups. Gero (1952) recorded an AR of 2.5 (measured from photographs) for the bottle-nosed dolphin, *Tursiops truncatus* and Fierstine measured an AR of 4.85 for *Delphinus bairdi* caught off Central America. To judge from the illustrations of various whales given by Slijper (1962), the above values are representative of all cetaceans. Walters measured an AR of 3.5 for a male bonito shark (*Isurus glauca*) caught off Santa Catalina Id, on September 15, 1966. The AR values for cetaceans and elasmobranchs are lower than those measured for most all scombrids.

The basis for the hydrodynamic perfection of the caudal fins of the advanced scombroids, and the hydrodynamic imperfection of the elasmobranch and mammalian hydrofoils, is to be found in the nature of the building materials available to the different animal groups. Scombroids, being actinopterygians, have ossified fin-rays and bone is a strong and rigid building material. Elasmobranchs have keratinized fin-rays and keratin lacks the strength and rigidity of bone. Cetaceans lack fin-rays and they strengthen their flukes by means of a system of muscle and collagenous ligaments and tendons (Parry, 1949a, 1949b; Slijper, 1962). Collagen has high tensile strength, but negligible rigidity. Thus, among the active aquatic vertebrates, only the actinopterygian fishes have been able to construct a hydrofoil of high efficiency; the others have been forced to make do with less efficient structures.

Nursall (1958b) noted that the AR varied nearly twofold in fixed specimens of striped pargo, whereas the rapidly swimming jacks and tunas had characteristically rigid caudal fins with a constant span. Bainbridge (1963) showed that the trout varies its caudal span about 30% when swimming. Our results support the theory that rapid swimmers have rather rigid fins; however, the barracuda which has been recorded at 27.6 mph (Gero, 1952), expands and contracts its caudal fin while swimming (Walters et al., unpublished data). Thus, a rigid caudal fin may indicate a fast-swimming fish, but not all fast-swimming fish have rigid caudal fins.

Nursall (1958b) speculated that AR and swimming ability could be correlated; for example, the yellowfin tuna (AR=5.2) may be a better swimmer than a black skipjack (AR=5.0), which in turn is a better swimmer than a sierra (AR=4.1) (AR values measured by Nursall). This is an overgeneralization, since both the wahoo and yellowfin tuna have similar burst speeds (Walters and Fierstine, 1964), but the wahoo has a lower AR (Table 4). Perhaps the yellowfin tuna has a higher cruising speed than does the wahoo. There is little known about scombroid life histories.

The AR of yellowfin tuna between 500 and 1000 mm in length is independent of fork length (Fig. 8). Since $AR = \text{span}^2 / \text{area}$ while span varies directly with body length, we expect AR to be constant unless the shape of the caudal fin changes ontogenetically. If it is assumed for all scombrid fish that the AR is independent of body length and of burst speed, then the AR must be dependent upon some other factor such as body shape. But the slender marlins (*Tetrapturus* spp.)

and sailfish are closest to the wahoo and sierra in body shape, yet their ARs are widely different. The chunkiest scombrids, the tunas and skipjacks have aspect ratios closest to the slender bill fishes. On this basis, the AR does not appear to have a simple relationship to body shape, size or burst speeds. As indicated earlier, our knowledge of the life histories of scombroids is meager and caudal fin AR may bear importance in overall swimming activity.

Table 4, organized according to descending aspect ratios (Table 7), nearly follows a classification scheme proposed by Kishinouye (1923) and modified by Berg (1940). The fish considered as primitive have the lowest aspect ratios whereas, the most advanced members have the highest aspect ratios.²

Osteology

The peduncular region is the most rigid portion of the scombrid's post-cranial body. The bony lateral flanges on the peduncular vertebrae hold this region rigid in the horizontal plane and the depressed neural and haemal spines eliminate movement in the vertical plane. Although this development of a bony peduncular keel is limited to certain members of the Scombridae, it does not

²It seems odd that the Istiophoridae should have evolved a highly efficient caudal fin of high Aspect Ratio while retaining rather unsophisticated muscular and skeletal systems whereas the Scombridae have evolved sophisticated muscular and skeletal systems but have less efficient caudal fins. But the two families exhibit different patterns of social behavior. Istiophorids seldom travel in schools whereas most scombrids school except when feeding. A solitary fish in the open sea travels through a medium in which fluid flow is either laminar or turbulent but if turbulent the turbulence is usually on a large scale, larger than the fish. Schooling fishes, however, are readily spotted near the sea surface at night owing to the brilliant phosphorescence generated by the school; these are called "fireballs" by California fishermen. Obviously, the water flowing through a school of fish is made turbulent on a small scale (turbulences smaller than the individual fishes) by the body shapes and swimming movements of the school members, thereby causing small organisms to luminesce. We conclude that schooling fishes must experience fluid flow phenomena entirely different from those experienced by solitary fishes. We therefore suggest that even though teleosts possess the building materials necessary to construct hydrofoils of high Aspect Ratio and high propulsive efficiency, it is beyond the capabilities of the vertebrate nervous system to control a high Aspect Ratio caudal fin under turbulent flow conditions, and schooling fishes must make do with less efficient but more stable hydrofoils of less than ideal Aspect Ratio.

TABLE 7. Regrouping of Aspect Ratios from Table 4 According to the Classification of Kishinouye (1923) and Berg (1940)

FAMILY	NUMBER OF INDIVIDUALS	RANGE OF AR VALUES	MEAN AR
Istiophoridae	5	7.86-10.26	9.44
Thunnidae	27	6.01- 8.70	7.41
Katsuwonidae	30	5.53- 8.36	7.28
Cybiidae	22	4.69- 7.01	5.98
Xiphiidae	2	4.19- 6.63	5.41
Scombridae	7	4.45- 5.77	5.18

Thunnidae includes the albacore, bluefin tuna and yellowfin tuna. Katsuwonidae includes the black skipjack, frigate mackerel, and skipjack tuna. Cybiidae includes the Pacific bonito, sierra, slender tuna, and wahoo. Scombridae includes only the Pacific mackerel.

mean that only the Scombridae have restricted peduncular movement. Some of the Carangidae have well-developed scutes (modified scales) which not only reduce lateral resistance of the water similar to the fleshy peduncular keels of scombrids, (Kramer, 1960) but may also keep the peduncle rigid.

Outside of the peduncular region, the greatest rigidity is found throughout the posterior abdominal and anterior caudal regions where the neural and haemal zygapophyses are long (Fig. 9). In the black skipjack and frigate mackerel this area of the vertebral column has broad elongate articulations that would greatly limit vertical movement. The neural zygapophyses would restrict movements in the horizontal plane.

The two regions that yield the greatest freedom of movement have the least intervertebral overlap (Fig. 11). These regions are just anterior to the rigid peduncle (the pre-peduncular joint) and just posterior to the rigid peduncle (the post-peduncular joint). This is analagous to the dual joint system of cetaceans (Parry 1949a, 1949b and Kramer, 1960).

The vertebral articulations of xiphiid and istiophorids indicate that their swimming movements differ both from the scombrids and from each other. The istiophorids have a stiff vertebral column and probably swim with their vertebral column acting as a spring (Rockwell, Evans, and Pheasant, 1938) except for a possible joint between the 22nd and 23rd vertebrae. The flattened neural and haemal spines probably offer greater surface area and a stronger base for the attachment of the lateral body musculature. The muscles which occupy this increased surface would produce a greater torsional stress across the intervertebral joints (Koch, 1917) and would necessi-

tate enlarged zygapophyses to counteract this new stress.

No detailed observations on the swimming movements of istiophorid and xiphiid fishes have been recorded. A striped marlin caught by the junior author off San Clemente I., California on October 10, 1966 was observed to swim with extremely sinuous body movements when it was brought up alongside the boat.

Structural rigidity of the caudal fin complex is maintained even though this is the region of a major joint. The neural and haemal spines of the last peduncular vertebra act as the axis of rotation for the procurent caudal fin rays. However, instead of the fin revolving about this point as though it were a rigid rudder, it develops a camber because the autonomous elements (hypural, neural spines, epural, uroneurals, etc.) allow for a curvature in the supporting base. The shorter procurent rays contribute most directly to the camber because they overlies the curvature of the autonomous supporting structures. The principal caudal rays do not contribute to the camber because they overlies the rigid hypural plate. The posterior caudal rays also contribute to the camber because they can act as flaps. These factors may explain why fish have retained the small autonomous elements in the caudal fin complex even though they have developed a hypural plate.

The retention of a continuous synovial cavity within the base of the caudal fin rays indicates that movement still exists between the rays and the hypural plate. This movement can occur only in a vertical plane and would occur when the span of the entire fin is increased or decreased. This means that one probably could expect aspect ratio changes during certain phases of the sweep of the caudal fin, or during a burst of swimming activity.

Myology

The shape and interfolding of the myomeres allow the waves of muscular contraction to pass smoothly along the body as the scombrid fish swims through the water (Nursall, 1956). Within a single contracting myomere the anterior cones exert tension on posterior vertebrae; one or more intervertebral joints lie between the two points, and thus, when a myomere contracts, the body flexes. Successively posterior myomeres are increasingly more elongate so that each successively posterior myomere acts upon more and more intervertebral joints. Consequently, a wave of contraction increases in amplitude as it travels posteriad.

It is significant that the bulk of the musculature in scombrids bypasses the peduncular region and inserts on the caudal fin rays by means of lateral tendons. In dorsal aspect, the outline of the peduncle is widest at the middle of the peduncular keel (if present) and tapers to fin thickness at the base of the caudal fin. The tendons follow this contour using the lateral edge of the bony keel as a guide. The bony keel serves as a pulley to increase the angle of pull of the tendons on the rays of the caudal fin and thereby increase the lateral power vector applied to the fin rays; if they entered the caudal fin at a smaller angle (more parallel to the caudal fin rays) the lateral power vector applied to the fin rays would be very small. These lateral tendons cross the pre-peduncular and post-peduncular joints. The posterior cones insert on the peduncle and are the only white muscles which can operate the peduncle independently of the caudal fin. Since the peduncle offers little lateral resistance to the water (Kramer, 1960; Walters, 1962) a small muscle mass can move it laterally through the water. The skin, which is reinforced by collagenous fibers, acts like a flexor retinaculum to keep the lateral tendons from bowstringing away from the body during the flexion of the pre-peduncular and post-peduncular joints.

It has not been determined how much of the lateral muscle mass is red muscle. However, Kishinouye (1923) and Kafuku (1950) have shown that the red muscle of scombrids is hyperdeveloped. George (1962) showed that the red muscle of the mackerel (*Rastrelliger kanagurta* Russell) is organized both histologically and physiologically for continuous, slow contractions, whereas the white muscle is organized for quick and fast contractions. George suggested that the red muscle is used during migrations and the white muscle is used for darting movements. Boddeke, *et alii* (1959) suggested a similar role for red and white muscle in a variety of fresh water fish. This means that the white muscle which inserts on the caudal fin by the stout lateral tendons may not actively contract during slow continuous swimming. Therefore, the red muscle part of the myomeres which inserts via the posterior oblique tendons onto all vertebrae anterior to the second peduncular vertebrae is responsible for the prolonged swimming.³ Anatomically, our observations can

support this view because a positive angle of attack of the caudal fin does not result from active tension in the myomeric musculature, but from the water pressure upon the fin. The resistance to stretch by the great lateral tendons probably serves to keep the fin from collapsing. Since the red muscle is part of each myomere and since the myomeres are connected to each other and therefore to the lateral tendons which insert onto the caudal fin, then it is quite likely that when the red muscle contracts it not only moves the peduncle, but it also actively moves the caudal fin. A pull by the entire myomere (or at least by the white fibres) would probably only serve to strengthen the contraction and to increase the angle of attack. No special muscle mass is necessary to refine the angle of attack to some desired value, since the fish can refine the angle of attack by bringing more or less white muscle fibers into contraction.

The amount of intrinsic caudal fin musculature is reduced in the scombrids (Nursall, 1963a). The interradiialis muscle, a tendinous remnant of the hypochordal longitudinal muscle, and possibly a few slips of the deep ventral flexor are the only remaining intrinsic caudal muscles. This great reduction of the intrinsic caudal musculature indicates that the scombrid is unable to abduct its dorsal and ventral principal caudal rays. The presence of interradiialis indicates scombrids can move the rays in a vertical plane (i.e., alter span). Since the lateral tendons insert on the dorsal and ventral principal caudal fin rays distal to the hypural plate (and therefore distal to the axis of rotation for each ray), the contracting lateral musculature would keep the span of the caudal fin maximal by drawing the dorsal and ventral principal rays forward. However, the middle caudal rays will be abducted. The interradiialis muscle, if this interpretation is correct, would then antagonize the lateral musculature and reduce the caudal fin span.

Nursall (1956) recognized that scombrids utilize a third class lever system with the lever arm approximately equal to the work arm. In order to maintain an equilibrium of forces (or a uniform swimming speed), the force produced by the lateral musculature must be equal to the work load, on the caudal fin (water resistance against the fin as well as drag elsewhere on the fish).

The myological variations exhibited by the var-

³Barrett and Williams (1965) measured the hemoglobin contents of the bloods of various scombrids and found that the xiphiids and istiophorids have 10.2-13.0 gms/100 ml whereas scombrids have 10.4-19.8 gms/100 ml; the skipjacks and tunas have 15.6-

19.8 gms/100 ml. Skipjacks and tunas, by virtue of their higher hemoglobin concentrations, are probably able to supply their red muscles with more oxygen, which would enable them to either swim faster or longer than other scombrids at a sustained speed.

ious scombrid fishes differ from each other only by degree, with the Pacific mackerel being the simplest and the tunas and skipjacks being the most advanced. The myomeres are more elongated and the lateral tendons are longer in the terete forms (tunas, skipjacks) than in the more slab-sided species (wahoo, sierra). This might indicate that the slab-sided species have a more sinuous movement than the terete forms. Since the slab-sided species have the highest vertebral counts (Table 5), this might support the idea that they have a more anguilliform movement.

The istiophorid and xiphiid pattern of the lateral musculature is quite different from that in the scombrids. The gently Σ -shaped myomeres with their additional myosepta would seem to indicate anguilliform rather than a carangiform movement. When hooked, istiophorids execute anguilliform motions but xiphiids do not (observed by V. W.). Absence of sinuous motion in xiphiids may reflect the longer head and more robust body. These fishes lack the hyperdeveloped red muscle and therefore lack the ability to undergo long continuous swimming like the scombrids.⁴

The intrinsic caudal musculature is very well-developed in the swordfish and has most all of the essential features of the generalized percoid, *Hoplostetrus guntheri* (as described by Nursall, 1963a). The istiophorids have a similar intrinsic caudal musculature, but it is simpler than in the swordfish. Well-developed caudal musculature would indicate individual movement of the caudal rays, however, it is inconceivable how the caudal rays of the istiophorids and xiphiids with their deeply forked bases and great hypural overlap could be abducted individually. Thus, the presence of intrinsic caudal musculature in the billed-fishes remains enigmatic.

Classification

The classification of the Scombridae is currently under extensive investigation and a preliminary review (Collette and Gibbs, 1962) has recently been published. This analysis unites the mackerels, tunas, and skipjacks into a single family, the Scombridae. The investigations of Collette and Gibbs are based on extensive, international effort and cooperation and show that many species range world-wide. For this reason and with little

variation, we have followed their preliminary scheme. An extensive taxonomic study of the tunas (Iwai, Nakamura, and Matsubara; 1965) supports the view that the Scombridae needs consolidation.

Berg, (1940) recognized the perciform Suborder Scombroidei to include the recent families, Scombridae, (mackerels), Cybiidae (wahoo, bonitos, and seerfishes), Xiphiidae (swordfish), and Istiophoridae (marlins, spearfishes, and sailfishes). He followed the suggestions of Kishinouye (1923) and placed the tunas (Thunnidae) and skipjacks (Katsuwonidae) into their own Order Thunniformes because of a peculiar subcutaneous vascular network. Most recent workers have not followed this separation (Schultz and Stern, 1946; Gregory, 1951; Bertin and Arambourg, 1958). Based on the preliminary revision of Collette and Gibbs (1962), Berg's classification of the living forms reduces to:

ORDER PERCIFORMES

SUBORDER SCOMBROIDEI

SUPERFAMILY SCOMBROIDAE

FAMILY SCOMBRIDAE

SUPERFAMILY XIPHIIDAE

FAMILY XIPHIIDAE

FAMILY ISTIOPHORIDAE

Berg (1940) placed the Suborder Trichiuroidei just before the Scombroidei and in it he included the Gempylidae (snake mackerels) and the Trichiuridae (cutlass fishes). Tucker (1956) showed that the gempylids and the trichiurids form a continuous phylogenetic series. Matsubara and Iwai (1958) give evidence that the gempylid, *Lepidocybium flavo-brunneum* (Serventy), forms a link between the Scombridae and the Gempylidae. For example, *Lepidocybium flavo-brunneum* shares with certain scombrids, the absence of canine teeth, the presence of many pyloric caeca, 31 vertebrae, and a fleshy peduncular keel. All other gempylids have canine teeth, have few pyloric caeca, have more than 31 vertebrae (34-39), and lack a fleshy peduncular keel. Since the genus *Scomber* has 31 vertebrae, Matsubara and Iwai felt that *Scomber* and *Lepidocybium* were closely related. Our observations show that *Lepidocybium flavo-brunneum* is not as similar to *Scomber* as the anatomical evidence of Matsubara and Iwai (1958) would lead one to believe. *Lepidocybium flavo-brunneum* has 32 vertebrae instead of 31, there is only one epural instead of two on the hypural plate, the caudal rays barely overlap the hypural plate, and the musculature is non-scombrid-like. Until more material is available, we

⁴Istiophorids and xiphiids characteristically "fin" at the surface and at these times they either swim extremely slowly or not at all (observations by V. W.)

follow Berg in placing the Gempylidae and Trichiuridae into the perciform Suborder Trichiuroidei rather than within the Suborder Scombroidei.

We find it untenable that the Xiphiidae and the Istiophoridae should be contained within the Scombroidei. The billed fishes share with the scombrids such highly specialized features as reticulated gills (only in *Acanthocybium solanderi* (Cuvier)) and caudal rays which greatly overlap the hypural plate (found in all scombrids). Both features may indicate evolutionary convergence, since overlapping caudal rays are known in such diverse oceanic fish as the luvarid (*Luvarus imperialis* Rafinesque), the carangids (*Megalaspis* and *Caranx*) and the hypochordal rays of the flying fishes (Order Atheriniformes, Rosen, 1964). The billed fishes share with the gempylids, *Ruvettus* and *Lepidocybium*, as well as with the shady dealfish (*Desmodema polysticta*: Order Lampridiformes) a peculiar tubular network and minute pores in their skin. Walters (1963) has hypothesized that this is a boundary layer control device which would help solve certain hydrodynamic problems.

The Istiophoridae and Xiphiidae have a low vertebral count (24-26), the development of bills, and large juveniles and adults have enamel on the most superficial layer of scales on the bill and body (Carter, 1919 and V.W. unpublished data). In addition, both families have two vertebrae in the caudal fin complex, they have 3 epurals, and both the lateral and intrinsic caudal musculature is distinct from the scombrids. Thus, on the strength of the foregoing discussion, we place the billed fishes in a separate perciform suborder, the Xiphiodei, apart but related to the Scombroidei and the Trichiuroidei.

The differences between the Xiphiidae and the Istiophoridae are numerous. The most fundamental differences are: 1) the swordfish has normal cube-like centra with small zygapophyses, whereas the istiophorids have elongate, hour-glass shaped centra that are united together by large struts, and 2) the swordfish has a non-depressible dorsal fin, a fleshy peduncular keel, no pelvic fins, and a flattened bill, whereas the istiophorids have a depressible dorsal fin, lack a fleshy peduncular keel, have pelvic fins and a bill which is round in cross-section. These fish should remain separate from one another under the Suborder Xiphiodei.

The classification used herein then stands as:

ORDER PERCIFORMES

SUBORDER SCOMBROIDEI

FAMILY SCOMBRIDAE

SUBORDER TRICHIUROIDEI

FAMILY GEMPYLIDAE

FAMILY TRICHIURIDAE

SUBORDER XIPHIOIDEI

FAMILY XIPHIIDAE

FAMILY ISTIOPHORIDAE

The fossil accounts of the various fish groups were not critically evaluated at this time. Much of the evidence is based on fragmentary material and many of the specimens appear to be incorrectly identified. However, it does appear that the Scombridae, Istiophoridae, Xiphiidae, and Gempylidae can be traced back to four early Eocene groups (Woodward, 1901). Questionable evidence places the fossil billed-fishes in the late Cretaceous. Since the late Cretaceous was the beginning of other perciform lines (Berg, 1940), it is possible that the scombrids, trichiuroids, and xiphioids diverged from a common ancestor at the time.

SUMMARY AND CONCLUSIONS

Locomotion in scombroid fishes was studied anatomically and experimentally using 150 specimens. Using a modified hook-and-line technique, it was determined that maximum acceleration measurements for a rapidly swimming yellowfin tuna (43.1 m/sec/sec) and a wahoo (35.9 m/sec/sec) were similar in magnitude to published values from a standing start for the trout (44.7 m/sec/sec) and the perch (52.0 m/sec/sec). However, the differences in the starting velocities between these two groups of fishes make direct comparisons impossible.

The swimming pattern of the wavyback skipjack is of the carangiform type with the body undergoing minimal yaw and the caudal fin undergoing an amplitude that reaches .30 times body length. Ciné film analyses of five sequences of wavyback skipjack suggest that the forward velocity varies directly with amplitude as well as with number of tail beats/sec.

The angle of attack of the caudal fin of the wavyback skipjack reaches its maximal value before it crosses the axis of progression. Maximal values of over 100° were recorded and the values for a complete tail sweep (from side to side) averaged 29.2°. These values are much higher than those published for the trout, dace, bream and goldfish (averages 13°) and are much higher than efficient values for the airfoil (11°). It seems therefore, that scombrids can achieve angle of attack values much higher than previously recorded.

The transverse velocity of the caudal fin is not constant, but reaches a maximal value after crossing the axis of progression. Since this position of the caudal fin is opposite to the angle of attack curve, it seems that the interrelationship of the transverse caudal velocity and the angle of attack functions to maintain a constant thrust. Another factor contributing to a constant forward velocity may be the lagging behind of the tips of the caudal fin when the remaining portion reverses direction at the lateral extreme of its sweep. This would suggest that the fin is never at zero transverse velocity.

The tips of the caudal fin in swimming scombrids lag behind the middle of the caudal fin (hypural base) during the transverse caudal sweep and is exactly the opposite dihedral of that published for the minnows. This dihedral of the scombrid caudal fin would promote turbulence at the caudal tips and thus supports the view of Walters (1962) that the small converging pair of V-shaped keels at the anterior base of the caudal fin serve to accelerate the flow at the hypural base to decrease caudal tip turbulence.

Caudal amputation experiments on living yellowfin tuna show that nearly 100% of the forward thrust comes from the caudal fin and that this thrust is not transferable to other parts of the body as has been shown for smaller freshwater fishes.

Studies on the aspect ratio ($\text{span}^2/\text{surface area}$) of the caudal fin show that the aspect ratio does not change with the fork length in adult yellowfin tuna and skipjack tuna. Aspect ratio values are higher than previously considered (7.7-10.2 for istiophorids) and approximate values for efficient high speed airfoils (8-10). The aspect ratio values seem to follow phylogenetic lines; the most primitive scombrids have the lowest values, whereas the most advanced scombrids have the highest values.

The span of the caudal fins in freshly killed scombrids can be altered, whereas the span of istiophorids is unalterable. However, anatomically it appears that in the scombrids, the fin is always at maximal expansion during normal contraction of the body musculature.

Analysis of the scombrid skeleton shows that there is a minimum amount of intervertebral

overlap in the regions where the greatest amount of bending occurs during swimming, whereas various structures are present to minimize intervertebral movements in other body regions. There are two main regions of movement, a pre-peduncular joint and a post-peduncular joint with the intervening peduncle held rigid. The resulting swimming movement is similar to that observed for cetaceans except that it is in the horizontal plane.

The structure of the caudal fin complex, caudal fin rays and the intervening synovial joint show that movement of the fin rays is restricted to a vertical axis which changes the span, except for the region of the autonomous vertebral elements (uroneurals, epurals, hypurals, etc.) of the caudal fin complex. It is in this region that camber is allowed in the caudal fin. The necessity for camber, may explain the retention of the autonomous elements of the caudal fin complex in various Teleostei.

The amount of lateral musculature in scombrids does not differ from that in other active fishes, however, the elongation of the myomeres and the hyperdevelopment of red muscle and tendons is unique. The interfolding of the myomeres enables a single myomere to act upon the caudal fin. During continuous, sustained swimming it is thought that the red muscle part of the myomeres acts directly upon the caudal peduncle through the posterior oblique tendons, and indirectly upon the caudal fin through the great lateral tendons to strengthen the myomeric contractions as well as to increase the angle of attack.

The bony peduncular keel, previously thought to serve as a site for muscle attachment, is shown to act as a pulley for the great lateral tendons, so that the direction of pull on the caudal fin by the tendons has a greater lateral power factor than if the keels were absent. In addition, the bony keels probably help stiffen the peduncle and serve as support for the fleshy peduncular keels.

The classification of the various scombroid fishes is re-evaluated in the light of many features that are related to locomotion. It is concluded that there are three separate suborders, the Trichiuroidei, Scombroidei, and Xiphiodei which probably diverged from related ancestors in late Cretaceous or early Cenozoic times.

LITERATURE CITED

- American Fisheries Society
1960. A list of common and scientific names of fishes from the United States and Canada. 2nd Ed. Amer. Fish. Soc. Spec. Publ. 2; 102p.
- Bainbridge, R.
1958. The speed of swimming fish as related to size and to the frequency and amplitude of the tail beat. *J. Exper. Biol.* 35:109-133.
1963. Caudal fin and body movement in the propulsion of some fish. *J. Exper. Biol.*, 40:23-56.
- Barrett, I. and A. Williams
1965. Hemoglobin content of the blood of fifteen species of marine fishes. *Calif. Fish and Game* 51 (3): 216-218.
- Berg, L. S.
1940. Classification of fishes both recent and fossil. (Reproduced in Russian and English in 1947). Ann Arbor, Mich., Edwards Bros., Inc., 517p.
- Bertin, L. and C. Arambourg
1958. Sous order des Scombroidei. P. Grassé, (ed.), Masson and Co., Paris. p. 2432 *In* *Traité de Zoologie*, Vol. XIII (Part 3), pp. 1813-2758.
- Boddeke, R., E. Slijper, A. van der Pelt
1959. Histological characteristics of the body-musculature of fishes in connection with their mode of life. *Proc. Koninkl. nederl. Akad. van Wetenschappen, Amsterdam*, Series C 62(5):576-588.
- Breder, C. M., Jr.
1926. The locomotion of fishes. *Zoologica*, 4: 159-297.
- Carter, J.
1919. On the occurrence of denticles on the snout of *Xiphias gladius*. *Zool. Soc. London, Proc.*, pp. 321-325.
- Clothier, C. R.
1950. A key to some southern California fishes based in vertebral characters. *Calif. Fish and Game, Fish. Bull.*, 79:3-83.
- Collette, B. and R. H. Gibbs, Jr.
1962. A preliminary review of the fishes of the family Scombridae. F.A.O. World Sci. Meeting on the biology of tunas and related species, La Jolla, Calif. July 2-14, 1962. Methodological paper, No. 1A, Section No. 1:1-10.
- Fitch, J. E. and W. L. Craig
1964. First records for the bigeye thresher (*Alopias superciliosus*) and slender tuna (*Allothunnus fallai*) from California, with notes on eastern Pacific Scombrid otoliths. *Calif. Fish. and Game*, 50:195-206.
- Ford, E.
1937. Vertebral variation in teleostean fishes. *J. Marine Biol. Assoc. of Unit. Kingdom*. 22:1-60.
- George, J. C.
1962. A histophysiological study of the red and white muscles of the mackerel. *Amer. Mid. Nat.*, 68:487-494.
- Gero, D. R.
1952. The hydrodynamic aspects of fish propulsion. *Amer. Mus. Nov.*, (1601):1-32.
- Godsil, H. C.
1954. A descriptive study of certain tuna-like fishes. *Calif. Fish and Game, Fish. Bull.*, 97:1-185.
- Godsil, H. C. and R. D. Byers
1944. A systematic study of the Pacific tunas. *Calif. Fish and Game, Fish Bull.*, 60:1-131.
- Gosline, W. A.
1960. Contributions toward a classification of modern Isospondylous fishes. *British Mus. Nat. Hist., Bull. Zool.*, 6:327-365.
1961a. The perciform caudal skeleton. *Copeia*, (3):265-270.
1961b. Some osteological features of modern lower teleostean fishes. *Smithsonian Misc. Coll.*, 142(3):1-42.
- Gray, J.
1933. Studies in animal locomotion. III. The propulsive mechanism of the whiting (*Gadus merlangus*). *J. Exper. Biol.*, 10: 391-400.
1953. How animals move. Cambridge U. Press, 144 p.
- Gregory, W. K.
1951. *Evolution Emerging*. New York, Mac Millan Co., (2 Vol.), 736 p.
- Gregory, W. K. and G. Conrad
1937. The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). *Am. Mus. Novitates*, (925):1-25.
- Harris, J. E.
1953. Fin patterns and mode of life in fishes. *Essays in Marine Biology*. Oliver and Boyd, Edinburg, pp. 17-28.
- Hubbs, C. L. and K. Lagler
1958. *Fishes of the Great Lakes Region*. Cranbrook Institute of Sci. Bulletin No. 26.
- Iwai, T., I. Nakamura and K. Matsubara
1965. Taxonomic study of the tunas. *Misaki Mar. Biol. Inst., Kyoto Univ., Spec. Rpt.*, 2:1-51.

- Kafuku, T.
1950. "Red muscles" in fishes. I. Comparative anatomy of the scombroid fishes of Japan. Japan Jap. J. Ichthyol., 1:89-100.
- Kishinouye, K.
1923. Contributions to the comparative study of the so-called scombroid fishes. College Agric. Imper. Univ. Tokyo, J., 8(3):293-475.
- Koch, J. C.
1917. The laws of bone architecture. J. Anat., 21:177-298.
- Kramer, E.
1960. Zur Form und Funktion des locomotion Apparates der Fishche. Z. Wiss Zool., 163: 1-36.
- LaMonte, F.
1946. North American Game Fishes. New York Doubleday, 202 p.
- Mago-Leccia, F.
1958. The comparative osteology of the scombroid fishes of the genus *Scomberomorus* from Florida. Bull. Mar. Sci., Gulf and Caribbean, 8:299-341.
- Matsubara, K. and T. Iwai
1958. Anatomy and relationships of the Japanese fishes of the family Gempylidae. College Agric., Kyoto U., Mem. Fish Ser., Spec. Number, June:23-54.
- Nursall, J. R.
1956. The lateral musculature and the swimming fish. Zool. Soc. London, Proc., 126: 127-143.
1958a. A method of analysis of the swimming of fish. Copeia, (2):136-141.
1958b. The caudal fin as a hydrofoil. Evolution, 12:116-120.
1962. Swimming and the origin of paired appendages. Amer. Zool., 2:127-141.
1963a. The caudal musculature of *Hoplopagrus guntheri* gill (Perciformes: Lutjanidae). Can. J. Zool., 41:865-880.
1963b. The hypurapophysis, an important element of the caudal skeleton, Copeia, (2): 458-459.
- Parry, D. A.
1949a. The swimming of whales and the discussion of Gray's paradox. J. Exper. Biol., 26:24-34.
1949b. The anatomical basis of swimming in whales. Zool. Soc. London, Proc., 119: 49-60.
- Ridewood, E. C.
1913. Notes on the South American freshwater fish, *Gastrolepecus*, and the common flying fish, *Exocoetus*. Ann. Mag. Nat. Hist., Ser. 8, 12(72):544-548.
- Robins, C. R. and D. P. de Sylva
1960. Description and relationships of the long-bill spearfish, *Tetrapturus belone*, based on western North Atlantic specimens. Bull. Mar. Sci., Gulf and Caribbean, 10(4): 383-413.
- Rockwell, H., F. Evans, and H. Pheasant
1938. The comparative morphology of the vertebrate spinal column. Its form as related to function. J. Morph., 63:87-117.
- Roedel, P.
1962. The names of certain marine fishes of California. Calif. Fish and Game, 48:19-34.
1963. The names of tunas and mackerels. Calif. Fish and Game 49(2):119.
- Rosen, D.
1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. Amer. Mus. Nat. Hist., Bull. 127.217-268.
- Schlichting, H.
1960. Boundary Layer Theory. New York, McGraw Hill Book Co., 4th Ed. 647 p.
- Schultz, L. and E. Stern
1946. The ways of fishes. D. Van Nostrand Co., Princeton, N. J. 264 p.
- Slijper, E. J.
1962. Whales. Hutchinson of London. Translated by A. J. Pomerans. 475 p.
- Starks, E. C.
1910. The osteology and mutual relationships of the fishes belonging to the family Scombridae. J. Morph., 21:77-99.
- Tucker, D. W.
1956. Studies on the Trichiurid fishes-3. A preliminary revision of the family Trichiuridae. British Mus. Nat. Hist., Bull. Zool., 4(3):73-130.
- Walters, V.
1962. Body form and swimming performance in the scombroid fishes. Amer. Zool., 2:143-149.
1963. The trachipterid integument and an hypothesis on its hydrodynamic function. Copeia, (2):260-270.
- Walters, V. and H. Fierstine
1964. Measurements of swimming speeds of yellowfin tuna and wahoo. Nature, 202 (4928):208-209.
- Woodward, A. S.
1901. Catalogue of the fossil fishes in the British Museum. Vol. 4. London, 636 p.

